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CALAMOPHYTON BICEPHALUM, A NEW SPECIES FROM THE MIDDLE DEVONIAN OF BELGIUM

SUZANNE LECLERCQ AND HENRY N. ANDREWS, JR.

ABSTRACT

This paper describes five specimens of Calamophyton found in the Middle Devonian of Belgium. Well preserved specimens have revealed the fact that both sterile and fertile appendages branch to form three-dimensional structures which are more complex than was formerly known for the genus. A new species, *Calamophyton* **bicephalum**, is established in which the sporangiophores bore twelve pendulous sporangia when all developed. SUZANNE LECLERCQ, Université de Liège, Laboratoire de Paléontologie Végétale, 7, Place du Vingt-Août, Liège, Belgium; HENRY N. ANDREWS, JR., Henry Shaw School of Botany, Washington University, St. Louis 30, Missouri.

INTRODUCTION

The fossil plant material on which the present study is based was collected by S. Leclercq in 1949 and 1952 from a Middle Devonian horizon in eastern Belgium. The Middle Devonian in Belgium is divided into the Couvinian and the overlying Givetian and our specimens come from the lower part of the latter.

The fossiliferous horizon is well exposed in one of two quarries (the north one) known locally as the "Carrières Brandt". They are situated on the upper part of the western slope of a hill lying 400 meters south of the junction of the rivers "La Gileppe" and "La Vesdre" at the small village of Goé which is in turn located about 30 kilometers east of Liège and 20 kilometers from Germany. The plant-bearing horizon is a lens-shaped deposit of numerous greenish and grey-blue shale layers 0.1 to 1.1 meters thick which are interbedded with arkose strata. It has been shown that the Middle Devonian in this region is a littoral formation deposited in shallow marine conditions (Aderca, 1932, p. 14; Liegeois, 1956, p. 98).

The fossil remains are abundantly distributed through the shales but the quality of preservation varies with the different layers. In most of them large specimens are encountered while in some the material is more fragmentary. The plants are found for the most part as well preserved compressions and occasionally as petrifactions in which the plant tissues are impregnated with iron hydroxide.

The "Goé flora" is a large one and includes many specimens referable to the Protoarticulatae. Some of them are large, splendid specimens representing the

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typical habit of *Calamophyton*; others are more fragmentary and it is problematical as to whether they should be referred to this genus or to *Hyenia.* It is, moreover, very possible that some will prove to lie outside the limits of both genera.

As is often the case in paleobotany our knowledge of these presumed early articulates has accumulated as the result of the work of several investigators and the quality of preservation and relative fragmentary state of the plants dealt with has varied greatly. Due chiefly to faulty preservation previous interpretations are not entirely correct and it seems fair to assert that, in general, the plants are not as well known as some of the published accounts would lead one to believe.

The present investigation was initiated in part from the discovery of the elaborate organization of the sporangiophore of the Upper Devonian sphenopsid cone *Eviostachya hoegi* Stockmans which was described in detail by Leclercq in 1957. The unexpected complexity of the sporangiophore "head" of this plant and the availability of well preserved specimens of the Middle Devonian Proto-articulates suggested the desirability of reinvestigating the latter.

Our study is based on several *Calamophyton* specimens which display the typical habit of that plant and the preservation is such that we have had an opportunity to contribute somewhat to a better understanding of the morphology of the leaves and spore-bearing appendages. The latter have proven to be much more complex than was supposed and we have been able to add appreciably to our knowledge of the branching pattern of the leaves. It is thus necessary to review the previous studies, at least briefly, particularly with reference to the presumed differences between *Calamophyton* and *Hyenia.*

Previous Studies

The genus *Calamophyton* was established in 1926 by Kräusel and Weyland with *C. primaevum* as the type species. It is reconstructed as a plant with an upright main stem which branches initially in a more or less digitate fashion; the primary branches, although predominantly monopodial, may also give rise to nearly equal dichotomies (see their plate 15, fig. 2). The leaves are once or twice forked and apparently less filiform than those of *Hyenia.* In view of our own description that follows it is perhaps significant to emphasize this difference as noted by Kräusel and Weyland (cf. their text figs. 26 of *Calamophyton* and 16a, 16b of *Hyenia*). Somewhat stouter, unforked sterile appendages were borne on the "main stem" and on the basal part of the primary branches. The fertile shoots are similar to those of *Hyenia* but each arm of the bifurcated sporangiophore usually bears but one sporangium (cf. their text fig. 27 of *Calamophyton* and text fig. 22 of *Hyenia*). Additional specimens were described by the same authors in their 1929 contribution.

In 1932 Aderca described and figured a fine sterile specimen of *Calamophyton primaevum* which was obtained at the same outcrop from which the new material described herewith was obtained. This specimen will be referred to again but it may be pointed out that it was erroneously determined as *Hyenia elegans* (see

Aderca's pl. 2, fig. 4), although the mistake was corrected by Kräusel (1932, p. 277). In 1940 Leclercq reported *C. primaevum,* as well as a new species, *C. renieri,* from the Middle Devonian of Belgium. She noted (see pp. 18, 33, 35) that most of the leaves in both species were more frequently divided and more filiform than those described for the above mentioned German specimens (cf. Leclercq, 1940, text fig. 9 with Kräusel and Weyland's figures).

The differences between the foliage of *Calamophyton primaevum* and *Hyenia elegans* as indicated by Kräusel and Weyland in the text figures cited above is quite striking; those of *Calamophyton* show a leaf that is narrow, almost wedge-shaped with a notched tip and it is this figure that has been used in textbooks (see, for example, Hirmer, 1927, fig. 400, 401; Arnold, 1947, fig. 55; Walton, 1953, fig. 38; Smith, 1955, p. 241; Magdefrau, 1956, fig. 61). Actually, Kräusel and Weyland's restoration does not bear out this exaggerated difference and in their description the leaves of *Calamophyton* are described as "schmallineal, ein- bis mehrfach gegabelt" (1926, p. 141). Unfortunately their specimens are no longer available for comparison but we shall present additional evidence which suggests that it is very doubtful whether the two genera can be distinguished on the basis of their leaves when only fragmentary specimens are available.

The fertile appendages (sporangiophores) of the two genera were described by Kräusel and Weyland as being very similar. In the case of *Hyenia* each branch of the sporangiophore is said to bear two or three sporangia while only one is found in the corresponding position in *Calamophyton* (cf. their text fig. 22 for *Hyenia* and text fig. 27 for *Calamophyton*). In her 1940 study of certain Belgian protoarticulates Leclercq noted that in *Calamophyton* each branch of the sporangiophore usually bore two sporangia; in the *Hyenia* specimens that she then had available the sporangiophores were noted to have several slender, bifurcating distal appendages. This suggested a greater complexity than was reported for the German fossils and is interesting in the light of our present observations which have been made on specimens of vastly better preservation.

As to the general habit of the plants in the two genera, although Kräusel and Weyland's original restoration of *Hyenia* (1926, pl. 16) shows a plant rather similar to that of *Calamophyton,* it was later recognized that the leafy and fertile shoots of *Hyenia* were borne on a relatively massive rhizome (Kräusel and Weyland, 1932, fig. 3). Studies that confirm this type of habit have been made on *Hyenia* specimens from Norway (Höeg, 1945) and Belgium (Leclercq, 1940) and these authors have both supplied restorations that indicate a conspicuous rhizome with slender upright shoots which are usually unbranched.

In summary it may be said, in the light of our present knowledge, that it is very doubtful whether the upright shoots of *Hyenia* can be differentiated from the distal parts of *Calamophyton* and only the general habit of the two remains as a distinguishing character that may be used with assurance. There is thus some question as to whether the two should be generically separated. It may also be noted that the anatomy of the two is not sufficiently well known to shed much light on the problem.

Materials on Which the Present Study Is Based; Study Technique

It is evident from the above summary that much remains to be learned about these fossil plants and it is particularly necessary that we have better preserved specimens in order to eliminate the doubt that exists concerning the morphology and taxonomy of these presumed early members of the articulate group. Our investigations have not solved all the problems but we have been able to make the following contributions which add to an understanding of the morphology of *Calamophyton*:

1. The sterile appendages (leaves) dichotomize two to four times and it is doubtful whether they can, with certainty, be distinguished from those of *Hyenia.*
2. The sterile appendages are three-dimensional in their branching pattern.
3. The fertile appendages are much more complex than previous accounts indicate.
4. Both fertile and sterile appendages may be borne on the same branch; there is, however, a marked tendency for the fertile appendages to be aggregated together into an apparently specialized branch system, but not into a clearly defined "cone".

The specimens that have been studied and the names assigned to them are as follows:

Calamophyton bicephalum Leclercq and Andrews, sp. nov.: Nos. 5011/609, 5012/337, 5009/588, 5007/346. In all cases the first of each dual number is the permanent one assigned to the fossil and the second is the number originally given in the field).

Calamophyton primaevum Kräusel and Weyland: No. 5006, previously described by Aderca, 1932, pl. 11, fig. 4.

Since the technique that is employed in the investigation of these fossils, although very simple, is perhaps not widely known, a brief description seems appropriate. The plants are preserved as compressions and both fertile and sterile appendages were three dimensional in their branching patterns. Since they also possessed some rigidity a single appendage may extend through several millimeters of sediment, thus it is not possible to apply a transfer technique and remove the entire specimen. What is revealed when the rock is first split gives at best a partial picture of an appendage as we shall point out in some detail in the descriptions. It is thus necessary to follow, through both part and counterpart, a selected appendage in order to determine its three-dimensional form. In the case of the fertile appendages, due to their small size and complex branching pattern, it often becomes necessary to excavate the matrix in terms of fragments only a few microns in diameter. Mechanical vibratory devices are much too coarse for such a delicate degagement and it is accomplished with steel needles and a small, light weight hammer. The size of the needles and the shape of the point will depend on the nature and delicacy of the operation. Invaluable information may thus be obtained with careful, painstaking work and the only costly element involved is the worker's time.

Gross Morphology of the Branch System

Reference will be made first to figure 1 (No. 5012/337) which is the largest

and most complete specimen insofar as the branch system as a whole is concerned. This consists of a major axis two cm. in diameter which divides repeatedly; since it is shown natural size in the figure it does not seem necessary to cite measurements for the various branch orders. It should be noted that the ultimate basal part of the plant is not preserved nor has this been identified in any other specimens. We shall, however, as a matter of convenience in description, refer to this basal part *of the specimen* as the *main stem*, and the first division members as the *primary branches*.

Although the initial branching of the main stem in a more or less digitate fashion seems to be highly characteristic of *Calamophyton* there is some variation in the organization of this cluster of primary branches. In figure 1 the main stem divides to form two unequal branches and the latter continue to dichotomize more or less equally throughout the length of the specimen. In the specimen shown at the upper left of figure 7 the main stem produces, almost simultaneously, seven primary branches of nearly equal diameter; the main stem of the specimen in the lower right of this figure starts with an equal dichotomy and the primary branches quickly divide again. In figure 14 the main stem produces three primary branches, although it might be interpreted as an initial unequal dichotomy in which the larger branch to the right dichotomizes again about two mm. above the initial division. The rather broad diagonal white band running through the upper part of the main stem represents a slight fault in the rock.

It is important to note that the main stem in fig. 1, and to a lesser degree the basal portion of the primary branches, shows the transverse bands which have been cited as a characteristic feature of *Calamophyton*. Several of these striations are preservation artifacts although some suggest an internal structure possibly comparable with the higher articulates; they are not evident in the upper branches of the specimen. Less clearly defined bands are present in the larger specimen (upper left) of fig. 7; we have not observed the transverse bands in the other specimens at our disposal. It also seems significant that in the basal part of this specimen (fig. 1) the striations are not correlated with any regularity in the distribution of the sterile appendages; thus if it is assumed that the transverse striations indicate nodes the leaves are scattered irregularly through the internodal region. Therefore we do not feel that there is sufficient evidence to regard this character as distinctive of *Calamophyton* and there is not adequate reason for comparing them precisely with the characteristic nodal structure of articulates such as the calamites and *Equisetum*.

The Sterile Appendages (Leaves)

A. On the main stem

The sterile appendages or leaves on the main stem are somewhat more robust than those borne higher up on the plant. Some *appear* as simple unforked structures, others are branched while some represent only the basal portions of branched leaves. The best preserved examples were found on specimens Nos. 5012/337 (fig. 1) and No. 5011/609 (part and counterpart, figs. 20 and 21). Some leaves of

No. 5012/337 are reproduced at a magnification of ×5 on plate 1; they represent the appendages shown in fig. 1 at points *a* (fig. 2), *b* (fig. 3), *c* (fig. 4) and *d* (fig. 5). It will be noted that the most profusely branched leaf reached four orders of divisions and was found higher up on the stem than the other examples cited.

One leaf was found on the main stem of the right hand specimen shown in figure 7 (point *a*) which contained a clearly defined vascular strand which could be followed almost to the tip. This leaf is shown enlarged in fig. 11 and a portion of the vascular strand is shown in fig. 10; the tracheids are apparently of the annular type.

In specimen No. 5011/609 (fig. 20) the leaves display a tendency toward a whorled arrangement but it seems significant to note that the transverse bands, previously considered as characteristic of *Calamophyton,* are not evident here and, as we have noted above, the transverse bands in the stem in fig. 1 are not correlated with any regular arrangement of the leaves.

B. On the branch system above the main stem

It is important to note that, prior to degagement, specimens give a misleading picture of the leaves since only about half of the appendage is exposed by the initial split of the rock specimen; this has been noted for other Devonian fossils in previous studies by Leclercq (1940, 1957). Consequently a considerable number of leaves were degaged or excavated with a small hammer and fine steel needles. Leaves were selected for detailed study that appeared to be well preserved and that were clearly identifiable on both part and counterpart. The leaf was degaged away, starting at the distal end, and followed toward the point of attachment to the stem until a branch was encountered. When this was done to both part and counterpart no question remained as to whether the entire leaf had been revealed. This resulted in the partial destruction of some leaves but the results obtained fully justified the procedure.

In several instances we were fortunate in obtaining the desired information without destruction of the leaf. Figure 8 shows a leaf from specimen No. 5009/588 (fig. 7, *b*) which appeared initially with the Y-shaped terminal portion (*a*) attached at point *b.* Due to a fortunate cleavage of the rock it was possible to remove this terminal portion intact and a comparable branch *c* was revealed directly underneath. The chip was glued in position as shown in the photo, thus preserving the entire leaf. In summary then, we are dealing with a leaf that forked at point *b* to form two equal branches (*a* and *c*) and the latter in turn dichotomize *at right angles* to the first dichotomy. A restoration of the leaf is shown in text fig. 1. Several other fortunate excavations of this sort revealed the same three-dimensional branching pattern without destruction of the leaf.

Several other examples, also taken from specimen No. 5009/588, will be mentioned to record variations in the gross morphology of these leaves:

Text figs. 1–5. 1. Restoration of leaf shown in fig 8. 2. Restoration of leaf shown in fig. 7 at *e*. 3. Restoration of upper leaf in fig. 13. 4. Restoration of leaf shown in fig. 12. 5. Restoration of leaves from specimen No. 5006 shown in figs. 15, 16.

5
1
4
3
2

Text figure 2 shows another leaf from the right hand specimen in figure 7 (*e*); this is similar to the preceding example but the initial dichotomy takes place closer to the proximal end and the secondary forking results in shorter branches.

Figure 12 shows a leaf attached at point *c* in figure 7. This was revealed initially, partly in side view and partly in surface view, and no further excavation was conducted. The leaf divides first at *a*, and then both branches divide at right angles to the first division at *b*. At the upper of the *b* divisions one of the two secondary branches was lost but this is indicated in the restoration drawing given in text fig. 4.

The upper portion of figure 13 shows another leaf from the same specimen (fig. 7, *d*). In this case the entire leaf was exposed initially and it is included to illustrate an example in which four orders of branching are evident; it is shown in text fig. 3 as an aid in interpretation. This represents the maximum degree of branching that we have observed in the leaves of *Calamophyton.*

Other leaves with four orders of branching have been carefully uncovered on the part and counterpart of specimen No. 5009/588 (figs. 9, 19). When well preserved they appear similar to the one shown in fig. 13 and text fig. 3. Another example (fig. 5) of one with four orders of branching is shown in the fertile specimen No. 5012/337 at point *d*. It is important to note that the leaves inserted in a similar position on a sterile branch system were small and wedge-shaped.

Many other examples could be cited but they would only duplicate the results obtained from those cited above. The ones chosen reveal the typical branching pattern and the variations that are encountered with reference to the number of orders of branching. There are numerous examples of the type shown in figure 8 and occasional variants from this pattern reveal a lack of forking of the secondary branches but the examples shown in figures 9, 12, 13 and 19 with three or four orders of branching seem to be most typical.

It is pertinent next to summarize the evidence that indicates the leaves are three-dimensional structures. In most cases it could be observed that the first dichotomy resulted in two branches that were directly superimposed; this is well shown in figure 8 where branch *a* was directly above branch *c*. In the second division, however, the resultant two segments lie apparently in the same bedding plane. In most cases where two or more orders of branching were present we are virtually certain that the orientation of successive branchings was at right angles, except possibly the fourth order. Additional evidence comes from examples such as the one in figure 12 (text fig. 4) in which irregular fracturing of the rock revealed a leaf initially in side and surface view.

There is next the question of the cross-sectional shape of these appendages; they are shown in the restorations as having been terete and we feel that there is substantial evidence to indicate that this was the case.

First, the leaves must have had considerable rigidity to have retained their three-dimensional form during fossilization. As many degagements reveal, one primary segment pushed down into the accumulating sediments so that the leaf as a whole was not flattened into one plane. It seems most unlikely that this would have been possible if the leaves had been thin, laminate structures.

Second, in well preserved specimens the thickness of the carbonaceous film is somewhat greater than might be expected if the leaves were laminate.

Third, for whatever correlation purposes it may be worth, it may be noted that several early land plants that are known in the petrified state (*Rhynia*, *Horneophyton*, at least some Coenopterids) possessed a shoot system in which the ultimate branches are terete.

The Fertile Appendages (Sporangiophores)

The quality of preservation of the fertile appendages varies considerably and this is due in part to their relative state of maturity at the time of fossilization. Our most significant evidence has come from specimen No. 5011/609 in which the preservation is excellent and the sporangiophores retain most or all of their sporangia. In contrast to this, specimen No. 5012/337 seems to be one in which dehiscence took place some time prior to fossilization; most of the sporangia are shriveled, fragmentary or missing.

Our basic description will, therefore, deal with a well preserved and apparently complete appendage from No. 5011/609. This is supplemented with a description of a second appendage of this specimen as well as several from No. 5012/337, partly to illustrate minor variations in the morphology of the fertile appendage and differences that result from the preservation of specimens at different states of maturity.

Specimen No. 5011/609

The fertile branch system as a whole is shown natural size in figure 21, the general morphology of the specimen being essentially the same as that found in the specimens shown in figs. 1, 7 and 14. It consists of an upright main axis of about 7 mm. in diameter which, at the top, divides into three primary branches which are of about the same size. One of the branches is dichotomized. The ultimate basal and terminal portions of the specimen are not preserved.

Below the point of division the main axis bears sterile, rigid appendages. These represent for the most part only the basal portion of the whole appendage; some are more complete and display a part of the more distal, divided portion. These organs are similar to the "basal leaves" found on the main axis of specimen No. 5012/337 (fig. 1).

The primary branches of the specimen are fertile throughout the portion that is preserved (fig. 29). They bear many whorls of sporangiophores only, there being no associated bracts. It has not been possible to determine the number of sporangiophores in a whorl; there are at least three and possibly as many as six. It was also difficult to decide whether, in successive whorls, the appendages were superimposed or alternate, though it is more probable that they were superimposed.

It is important to note that here, as in the case of the sterile appendages, the initial exposure of the specimen gives a misleading picture of the general morphology of the sporangiophore. The latter is a three-dimensional structure and half or more of it may be covered by the rock matrix. In order to be sure of

arriving at a correct understanding of the sporangiophore many of them were carefully uncovered under a binocular microscope using needles and a light weight hammer as described above.

Successive stages in the degagement of a selected sporangiophore are illustrated in figures 23 to 27. Figure 22 represents the counterpart (specimen No. 5011/609B) of the initial stage shown in fig. 23. As an introduction to the detailed description it may assist the reader to note briefly the over-all branch pattern: the fertile appendage divides into two segments or "heads" (referred to as upper and lower), each of which bore three short side stalks and each of these in turn terminates in a pair of sporangia; the distal tip of each of the two segments is usually bifurcated but not always so. Thus the sporangiophore as a whole, composed of two similar heads, supports twelve sporangia if all develop.

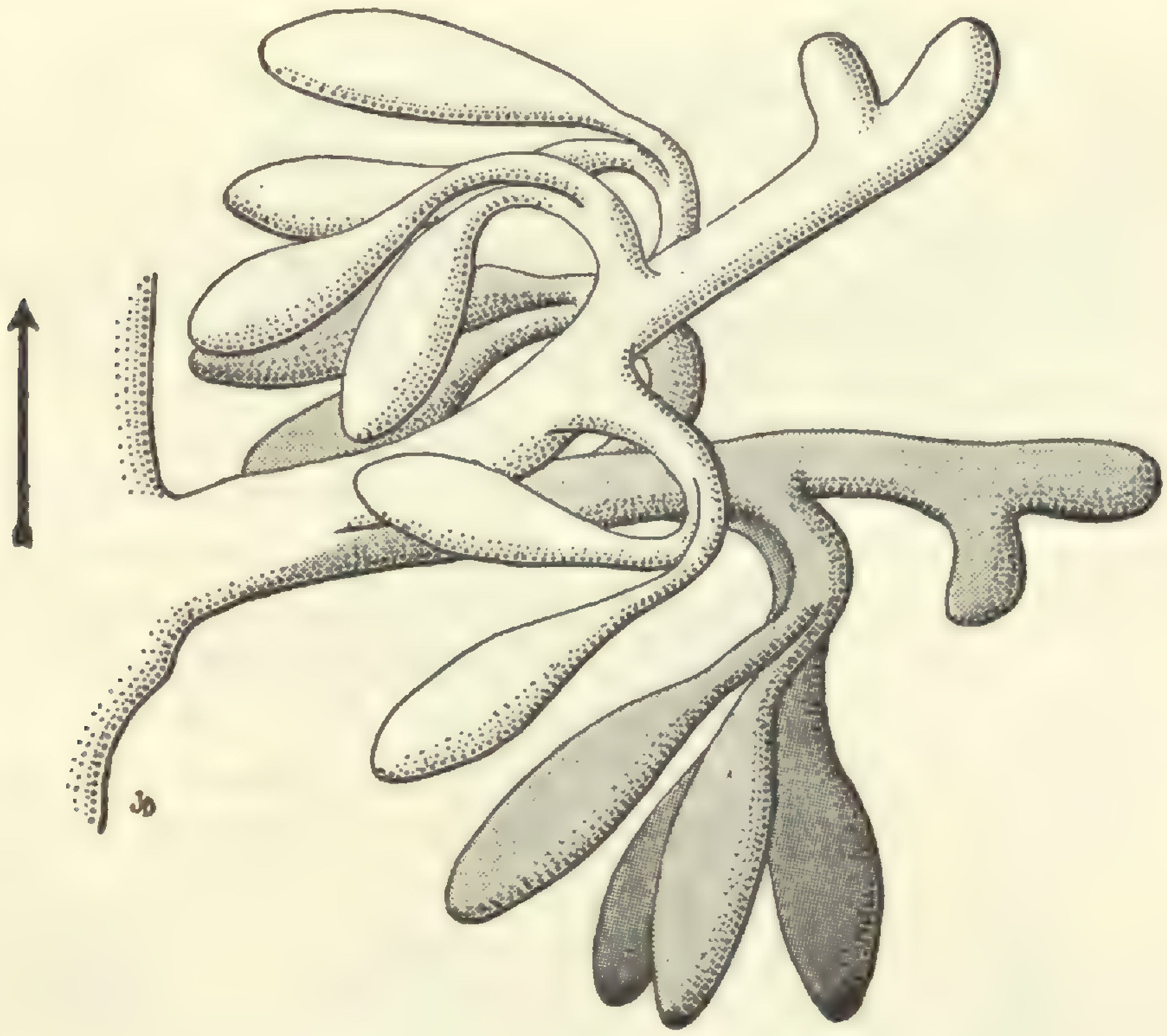
In figures 22 and 23 the upper segment (I) is shown from its base up to the ultimate preserved tip. This segment supports two side stalks, A and B, which are attached on either side at slightly different levels; two sporangia are borne on each stalk (fig. 23 and text fig. 6). Figure 24 reveals the third stalk, C, of the upper segment and one of its sporangia is visible; the second one is still overlain by stalk B although its distal part appears beside the two sporangia of the B stalk. Text figure 6 shows this upper segment or head with the three bifurcated stalks and their six sporangia in the position in which they were preserved.

In figure 24 a portion of the lower segment or head may be seen behind the upper one. Figure 25 shows the lower segment (II) in connection with segment I as well as the three stalks A, B, and C, which are borne by it (segment II); this is also shown in text figure 7. Stalk A has two sporangia in connection; stalk B appears with one sporangium attached and the second lies under segment I; stalk C is just coming into view at this level. In figures 25, 26 and 27 the second sporangium of stalk B has been revealed by removing parts of segment I. Stalk C, which was recurved under segment II, has been uncovered by destroying parts of the latter; it is now clearly revealed and has one sporangium suspended in an anatropous position on each of its two divisions or pedicels. Text figure 7 shows this lower segment (II) with its three bifurcated stalks and their six sporangia.

Text figures 6 and 7 when superimposed show the entangled stalks and sporangia of the entire sporangiophore as it was embedded in the sediment; text figure 8 is a reconstruction of the sporangiophore as we believe it appeared before fossilization and in natural position.

Thus, in summary, the sporangiophore was a small, adaxially inclined appendage attached to the branch axis. At a point about one third of the way from its proximal end the sporangiophore branched into an upper and lower segment. Each segment was erect and rigid and supported three short side stalks fixed at two different levels; the first stalk was given off at a different level than the two others which appear generally to be given off simultaneously. Each of the three stalks is slightly bifurcated at its tip with a sporangium attached to each bifurcation. Usually the distal, rigid portion of each segment of the sporangiophore terminates in an irregular dichotomy.

The sporangia were cylindrical sacs 2.0–2.7 mm. long and 0.5–0.7 mm. in



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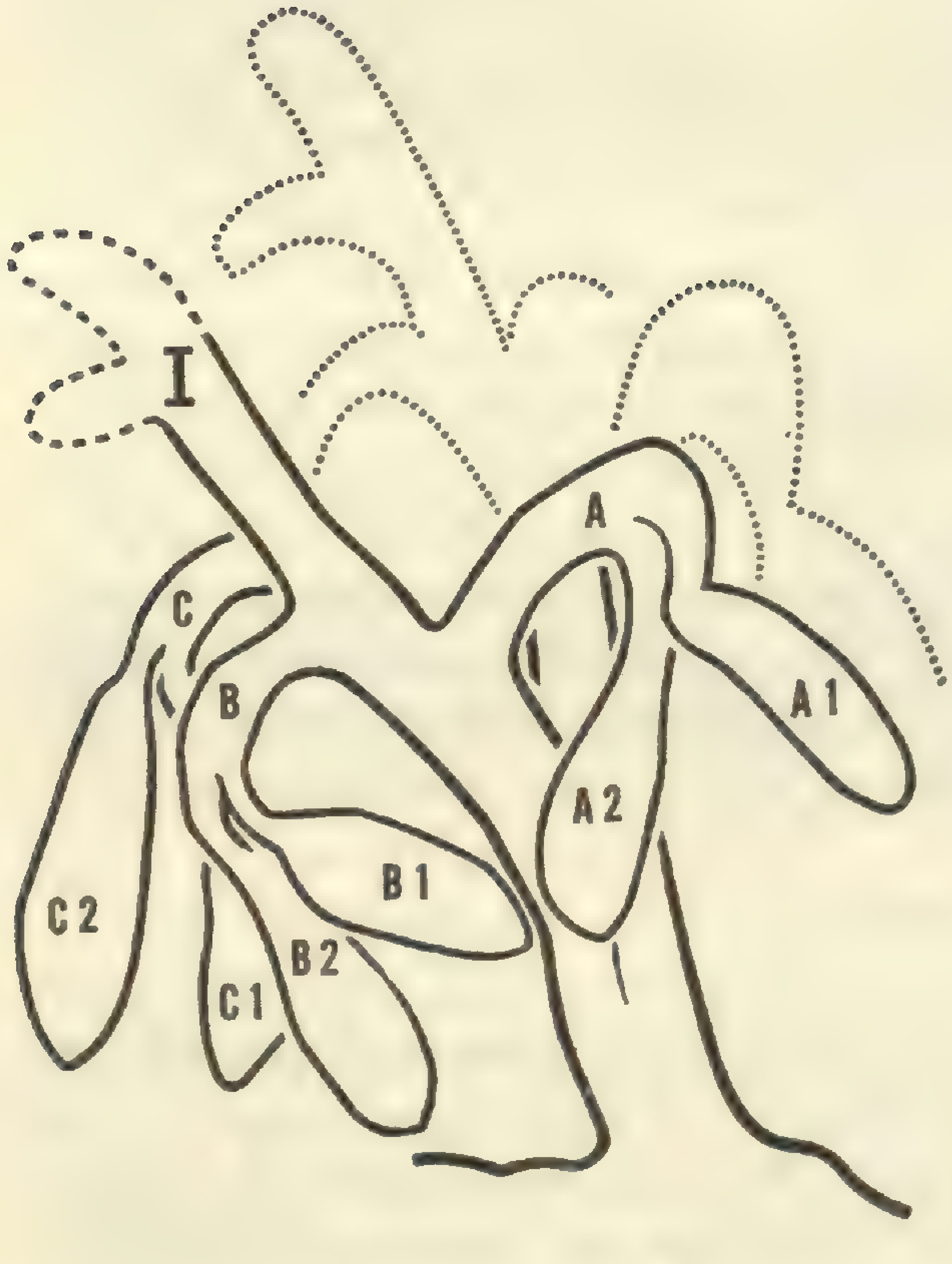

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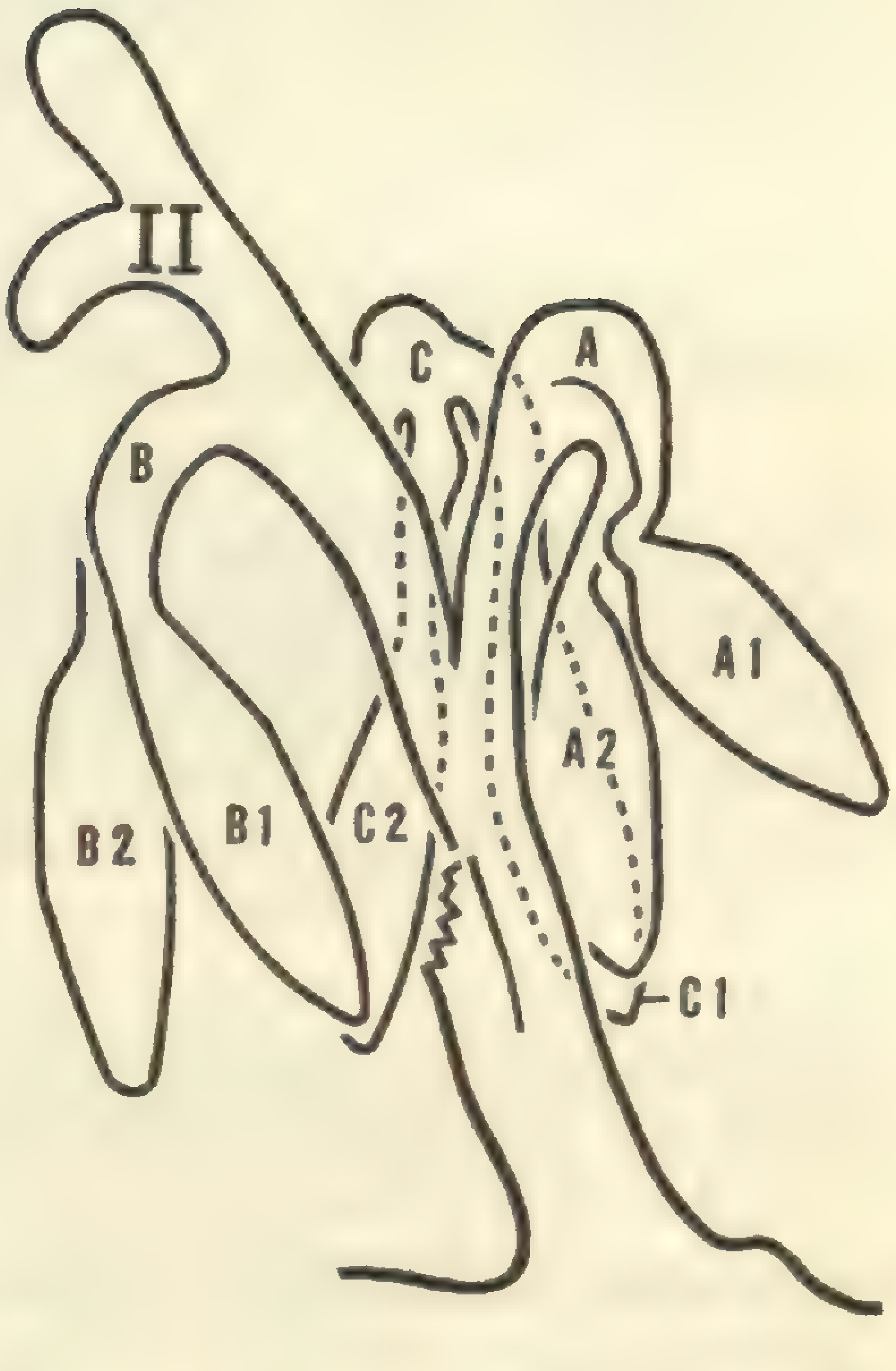

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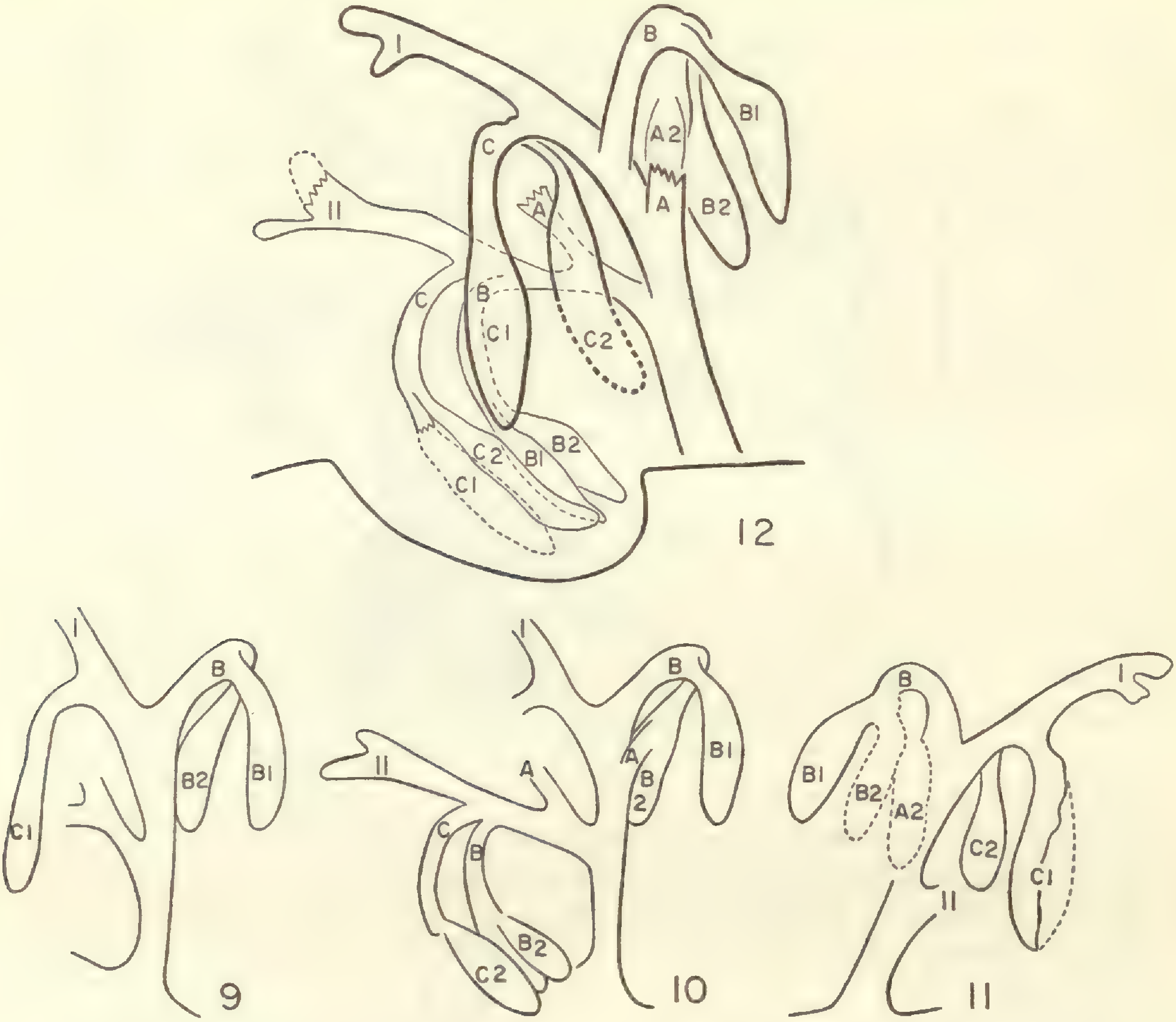
Text figs. 6–8. 6. Upper segment of sporangiophore (I) shown in figs. 23, 24 (specimen No. 5011/609. 7. Lower segment of same sporangiophore (II); see figs. 25–27. 8. Restoration of same sporangiophore. Arrow points toward apex of specimen as a whole.



Text figs. 9, 10. Stages in the excavation of a sporangiophore of specimen No. 5011/609; see also fig. 31. Text fig. 11. Counterpart of same appendage; see also fig. 30. Text fig. 12. Semi-restoration of same sporangiophore. Detailed explanation in text.

diameter and pointed at the distal end. They were apparently strongly constructed for despite the entangled position in which they occur they are often neither broken nor opened. It is possible that the wall of the sporangium was rather thick, perhaps as a result of several layers of cells or having been fossilized when immature; the latter seems most likely.

The mode of dehiscence has not been positively ascertained. Careful examination of the sporangia on the holotype specimen (No. 5011/609) has revealed no distal pore but on a few sporangia a median longitudinal line is found on the ventral side (fig. 28) which may represent the place of dehiscence.

It is evident from the numerous sporangiophores we have studied that their organization was essentially the same throughout; there are, however, some slight variations and in view of the rather surprising complexity of the fertile appendages as contrasted with previous accounts of Calamophytons it seems pertinent to supplement the description given above with somewhat briefer considerations of several other examples.

Text figure 9 is a camera lucida drawing of an appendage (No. 5011/609) prior to any treatment. The sporangiophore stalk divides into the two divisions; a considerable part of I is present but only the basal part of II. Referring to segment I, branch B is shown with its two sporangia B1 and B2 and one sporangium of the C branch is present. In order to expose segment II, which appeared to dip down into the rock, sporangium C1 was degaged away; after working through the sediment underneath sporangium C1 the II segment was revealed as shown in text fig. 10 and fig. 31. Three branches (A, B and C) were found departing from segment II. Branch C terminates in a single sporangium, C1, but judging from its mode of attachment this is one of an original pair; branch B is terminated by one clearly defined sporangium (B2) and there appears to be another beneath it; the third branch (A) could not be followed.

Text figure 11 and fig. 30 show the counterpart of the appendage; only segment I is present. The sporangia B1, B2 and C1 are readily correlated with their position as shown on the other face of the specimen (text fig. 9); there is some question as to the sporangium labeled A1 and a fifth one appears to the right of sporangium B2 whose position on the segment is undetermined.

Text figure 12 brings this information together as a semi-restoration. It may be noted that there were not less than eight sporangia borne by the entire appendage and the number was probably closer to ten or twelve.

Specimen No. 5012/337

Some significant information was obtained from this specimen (fig. 1) concerning the general branching pattern of the fertile appendages but, as noted above, very few sporangia could be identified intact due to the fact that dehiscence had apparently taken place some time prior to fossilization. It should be noted that there is no counterpart of this specimen; when it was found during the quarrying operations an extended search was conducted for the other side but it was apparently completely shattered and lost.

The three sketches shown in text figs. 13–15 show an appendage before and after degagement, and a semi-restoration respectively. The initial appearance was essentially as shown in text figure 13 aside from a slight amount of degagement that was necessary to expose branches B and C. The segment was then degaged away, starting at the distal end and extending down to the point indicated by line ---o. The underlying segment (II) was then detected and when completely excavated it appeared as shown in text fig. 14.

The semi-restoration of this appendage (text fig. 15) thus shows it as consisting of two main branches, I and II; II produces at least two secondary branches and terminates in a forked tip; I produces three secondary branches. All of the sporangia had been shed prior to fossilization.

A second example (fig. 6 and text fig. 16) is included since it gives some interesting information concerning the variation in the general morphology of the fertile appendages and particularly the ultimate terminations. It is virtually certain that the upper portion was attached as indicated by the dotted line but this was not positively demonstrated. The essential features of this appendage

seem to be as follows: the main stalk branches into two segments which in turn divide, each giving off several side branches, and terminate in unforked distal tips.

Although specimen No. 5012/337 is the largest one in the collections and the most completely preserved, with reference to the main branch system as a whole, none of the ultimate terminations of the branches are preserved; these probably extended out at least 10 or 15 cm. beyond what is shown in the photo (fig. 1). The ultimate appendages, both sterile and fertile, are for the most part rather poorly preserved and we interpret it as a plant, or portion of a plant, that had shed its spores and undergone partial decay prior to fossilization. Several fertile appendages are sufficiently well preserved as to offer evidence of their relationship with the new species *C. bicephalum.*

Diagnosis

Calamophyton **bicephalum** Leclercq and Andrews, sp. nov.

Plants consist of a main stem, the basal portion of which is unknown, which divides in a digitate fashion into two to several branches; these branches in turn divide in more or less equal dichotomies. Transverse striations are occasionally present on the main stem and lower portions of the primary branches. The shoot system, above the main axis, appears to be predominantly fertile or sterile. The sterile appendages (leaves) are somewhat more robust on the main stem than above, with a single vascular bundle, and dichotomize one to four times in a three-dimensional pattern and attain a length of about one cm. Fertile appendages are aggregated to form a specialized branch but not in definite cones; a fertile appendage consisted of a basal stalk which divided into an upper and lower segment; each segment bore three short side branches which terminate in a slight bifurcation with a pendulous sporangium attached to each, resulting in a total of twelve sporangia; each of the two main segments terminates in a short dichotomy. Sporangia are cylindrical, pointed at the distal end, 2.0–2.7 mm. long by 0.5–0.7 mm. in diameter, with possibly a line of dehiscence on the ventral side.

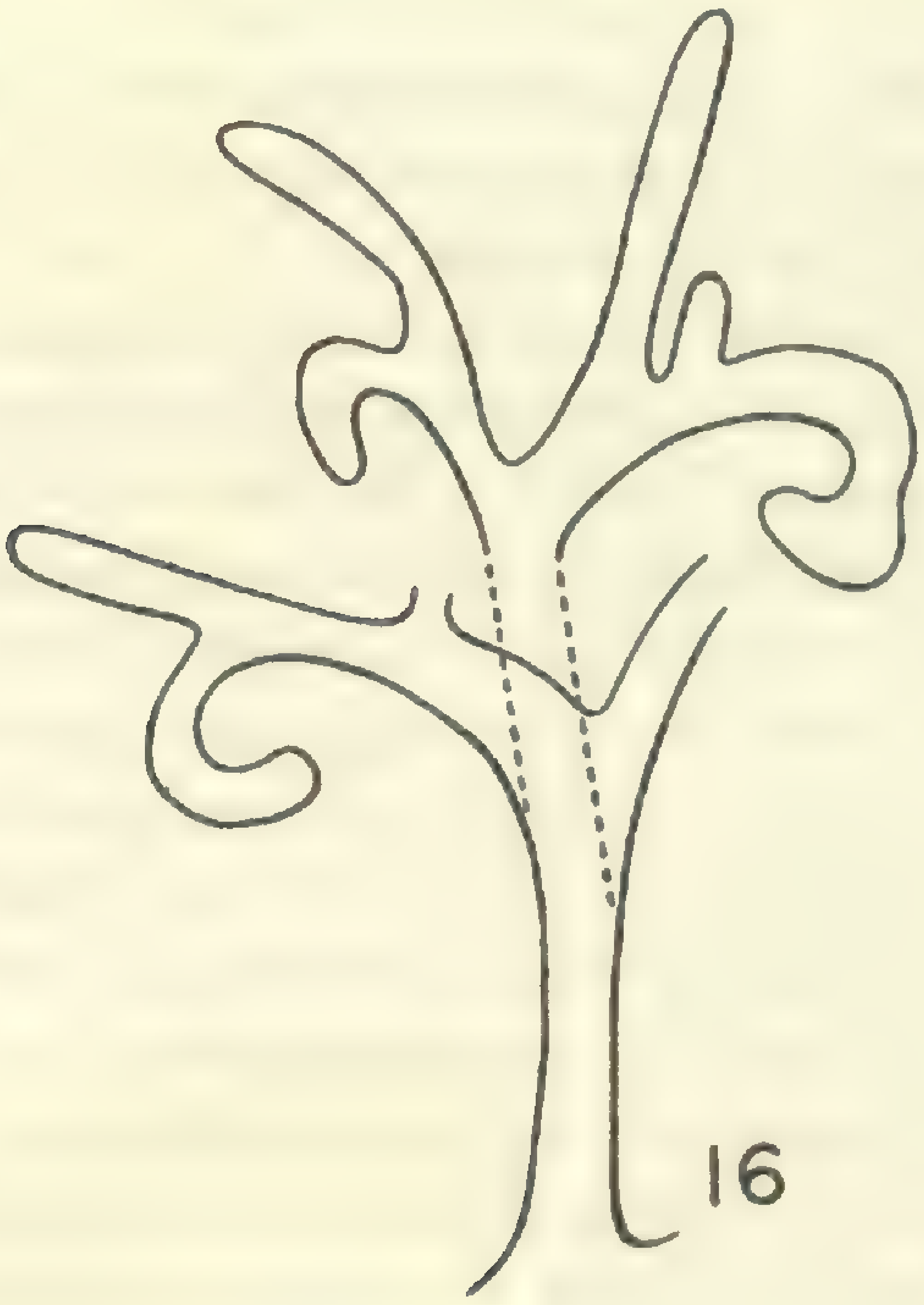
Holotype: No. 5011/609. Paratypes: No. 5012/337, No. 5009/588. All preserved in the Laboratoire de Paléontologie Végétale, Université de Liège.

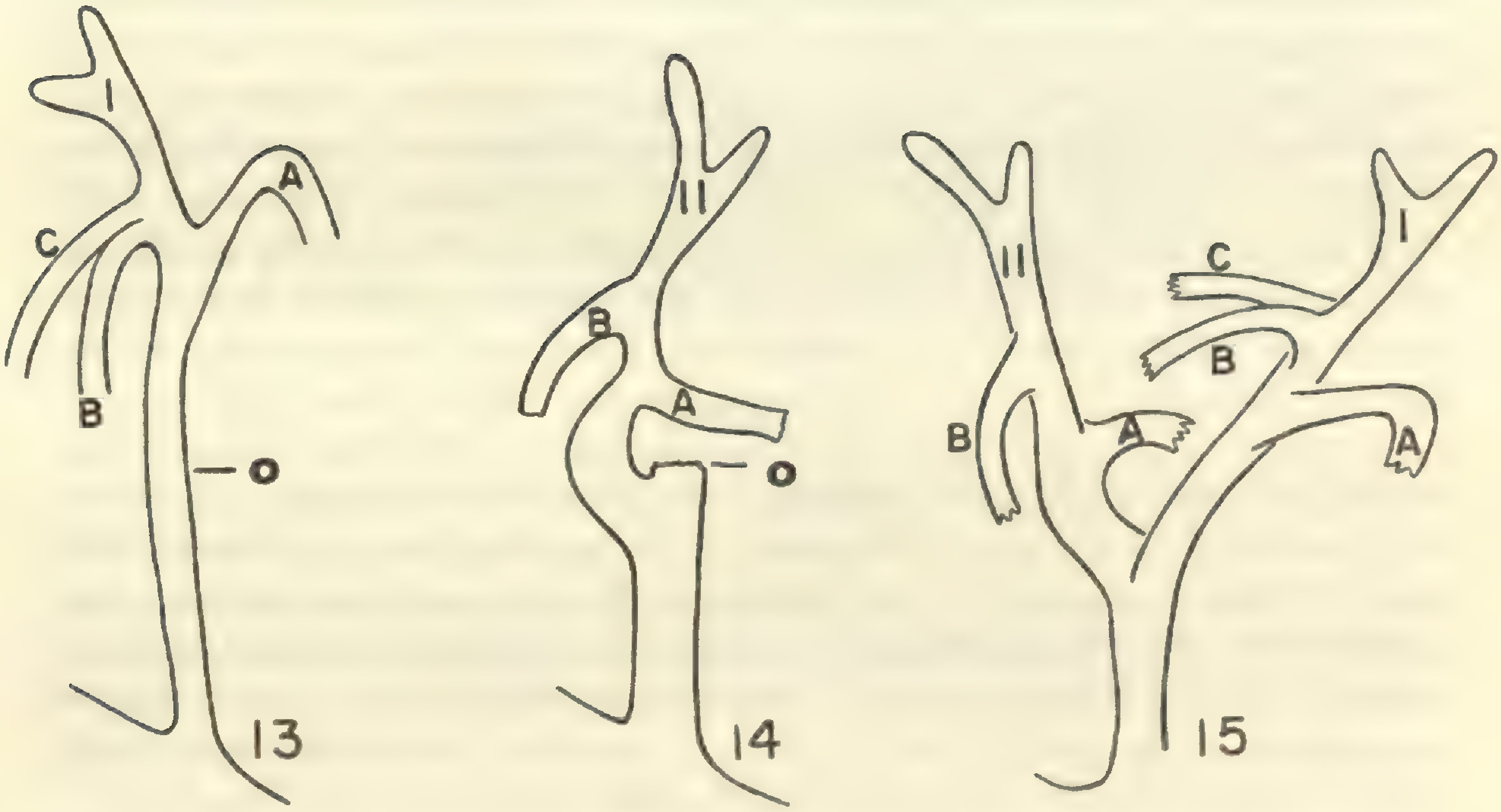
Horizon: lower Givetian, Middle Devonian.

Locality: Carrières Brandt (north quarry), Goé, Belgium.

Discussion

With the exception of the general organization of the branch system the new species of *Calamophyton* described here presents characters, particularly in the nature of the ultimate fertile and sterile appendages, that are quite new. In these features our plant differs sharply from *Calamophyton* as portrayed in all recent text-books. It was quite surprising to find these appendages so complex and it might be supposed that we are actually dealing with plants that should not be identified with this genus. Yet it may be noted that our specimens showed, on the initial split of the rock, rudimentary leaf-like organs (sterile appendages) which are small and once or twice divided apparently in one plane as previously





Text figs. 13–16. 13. A fertile appendage from specimen No. 5012/337 as it appeared originally. 14. Same appendage with segment I removed and underlying segment (II) revealed. Appendage I was formerly attached at break indicated by line ---o. 15. Partial restoration of same appendage. 16. Another appendage from specimen No. 5012/337. Detailed explanation in text.

described for *C. primaevum*. The same holds true for the sporangiophore; for example, these structures give the impression before degagement (figs. 22, 23) of being once forked and in only one plane. This aspect is apparently very similar to the sporangiophore of *C. renieri* (Leclercq, 1940) with the difference that the

small axis of the sporangiophore of *C. bicephalum* is prolonged as an erect appendage. Thus, in order to determine whether *C. primaevum* K. and W. actually had three dimensional leaves a specimen of this species (figs. 17, 18) formerly described by Aderca (1932) was selected for re-investigation.

Figure 15 shows two leaves that were selected as they appeared initially; both dichotomize and of the two resultant branches the left one in both undergoes another forking and, in the case of the lower leaf the left fork is again apically notched. Beginning at their apical extremeties the two leaves were degaged away down to the point indicated by the lines o----o, at which point a branch was found dipping down into the rock matrix. When completely exposed these underlying branches appeared as shown in figure 16 distal to the line o----o. The latter were thus directly beneath the branches shown in figure 15 and in both leaves the second dichotomy was at right angles to the first; these leaves are shown restored in text figure 5. Thus, in view of the identical morphology found in *C. bicephalum* we consider the three dimensional branching to have generic value.

The prominent characters of *C. bicephalum* are the three dimensional sterile and fertile appendages. The former was a fairly rigid, terete structure with somewhat varied form; wedge-shaped ones, notched at their apex, were found along the lower portions of the primary branches. Higher up the branching of the leaf became more pronounced until the "mature" stage, characterized by four orders of branching, was attained. Attention may be called to the fact that such mature leaves were found on the lower portion of the primary branches of *fertile* twigs.

It may next be of interest to consider the possible homology of the sterile and fertile appendages. In 1936, Eames noted that "from the evidence provided by *Hyenia* and *Calamophyton* it is apparent that 'leaves' and the fertile tips in this group are homologous". Our study indicated that this is undoubtedly true if one compares a "mature" leaf with a sporangiophore. The latter divides into two main branches, referred to previously as superior and inferior segments, which may correspond to the initial dichotomy of the sterile appendage. Beyond this point the fertile appendage is more complex in that each segment produces three side branches each of which bears a pair of sporangia while the segment proper is elongate and usually terminates in a forked apex. Whether or not the sterile appendages may be termed "leaves" is perhaps a matter of opinion but there would seem to be no doubt that they functioned as such.

The present study is an initial one dealing with the fossil plants from the Goé locality. The difficulty of working with Devonian plants is emphasized by this investigation but in no less degree it is demonstrated that reliable information may be obtained from such ancient land plants when they are well preserved.

It seems pertinent to add a few comments concerning previous work with both *Hyenia* and *Calamophyton* since they are undoubtedly closely related. Of the several species of these two genera that have been described to date none is known in its entirety.

The problem of making significant comparisons with previously described species is rendered difficult by the fact that during the recent war the material

described by Kräusel and Weyland (1926, 1929, 1932) was destroyed although two fragments of the fertile branch system of *C. primaevum*, from Dr. Kräusel's collections, are preserved in the Department of Geology of the University of Cologne. The two fragments on which *C. renieri* (Leclercq, 1940) is based are preserved at the University of Liège. In the light of what has now been found in *C. bicephalum* it may be desirable to rework, with the degaging technique, the available material of the two other species to try to determine the real value of the three specific epithets. It is, however, questionable whether the remaining specimens of the earlier described species are sufficiently well preserved to allow effective comparison, consequently our only course seemed to be to assign a new specific name to the Goé specimens.

In the light of what is now known it seems safe to assert that the only dependable difference between *Hyenia* and *Calamophyton* lies in the general habit of the two. Even this is complicated by the fact that we do not know anything about the basal part of the shoot system of *Calamophyton*. Our specimens do, however, suggest a habit that may be worth a few words of speculation. It seems likely that *C. bicephalum* consisted of upright shoots that were predominantly fertile (fig. 21) or sterile (fig. 7, lower right). If this was the case it seems unlikely that the fertile shoots would have had sufficient photosynthetic tissue to have maintained themeselves independently. In explanation it may be supposed that both were borne either on a common erect small "trunk" that would have given the plant a shrub-like appearance, or they were borne on a common rhizome with a relationship comparable to that found in the modern *Equisetum arvense*. It is expected that further studies of the Goé fossils will contribute toward solving this and other problems relating to both *Calamophyton* and *Hyenia*.

Summary

The material on which this study is based came from the lower Givetian (Middle Devonian) of Belgium.

A new species, *Calamophyton bicephalum* Leclercq and Andrews, is created in view of the complexity of the fertile appendages which contrast with homologous structures in the previously described species *C. primaevum* Kräusel and Weyland and *C. renieri* Leclercq.

The investigation has dealt chiefly in elucidating the structure of the sterile and fertile appendages.

The sterile appendages (leaves) are shown to be three dimensional organs that forked once (young leaves) to four times (mature leaves) and were probably rather rigid and terete in cross section. The three dimensional structure of these appendages is considered to have generic value.

The fertile appendage branched into upper and lower segments; each was erect and supported three curved side stalks attached at slightly different levels; each of these stalks terminated in a pair of pendulous sporangia. Thus the entire appendage bore twelve sporangia when all developed. The sporangia were cylindrical and pointed at the distal end, with possibly a line of dehiscence in the ventral side.

Acknowledgements

Je désire exprimer ma gratitude au Fonds National de la Recherche Scientifique de Belgique pour les deux campagnes de fouilles qu'il a subsidiées en 1949 et 1952 et au cours desquelles j'ai récolté le matériel ici étudié.

Je remercie le Patrimoine de l'Université de Liège qui m'a permis de recevoir le Professeur Henry Andrews pendant quatre mois à mon laboratoire.

A Monsieur J. Damblon vont mes sincères remerciements pour l'attention et le soin avec lesquels il a exécuté la reconstitution du sporangiophore représenté figure 8 du texte.

Je suis particulièrement reconnaissante à Monsieur José Lewalle, Assistant, et à Monsieur Maurice Discry, Préparateur-technicien, de l'aide continue qu'ils ont apportée à l'exécution des nombreux documents photographiques nécessités par cette étude. (Professeur S. Leclercq)

This investigation was carried out during my tenure as a Fellow of the John Simon Guggenheim Memorial Foundation; thanks are also due the National Science Foundation for aid in defraying publication costs and in other ways. (HNA)

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Explanation of Plate

PLATE I

Calamophyton bicephalum Leclercq and Andrews
Figures 1–6: specimen No. 5012/337

Fig. 1. A large specimen shown natural size. Figs. 2–5. Sterile appendages taken from points *a–d*, respectively, on specimen shown in fig. 1; all magnified × 5. Fig. 6. A partially preserved fertile appendage; see also text fig. 16 and description in text (p. 14); magnified ×5.

LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

Explanation of Plate

PLATE II

Calamophyton bicephalum Leclercq and Andrews
Figures 7–13: specimen No. 5009/588

Fig. 7. Two specimens shown natural size. Fig. 8. Leaf taken from point *b* in fig. 7; × 5. Fig. 9. Leaf showing four orders of branching; × 5. Fig. 10. Portion of vascular strand from leaf shown in fig. 11; × 62. Fig. 11. Leaf with vascular strand preserved from point *a* in fig. 7; × 3. Fig. 12. Leaf from point *c* in fig. 7; × 5. Fig. 13. Leaf showing four orders of branching from point *d* in fig. 7; × 5.

LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

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LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

Explanation of Plate

PLATE III

Calamophyton bicephalum Leclercq and Andrews

Fig. 14. Specimen No. 5007/346. ×1.

Calamophyton primaevum Kräusel and Weyland

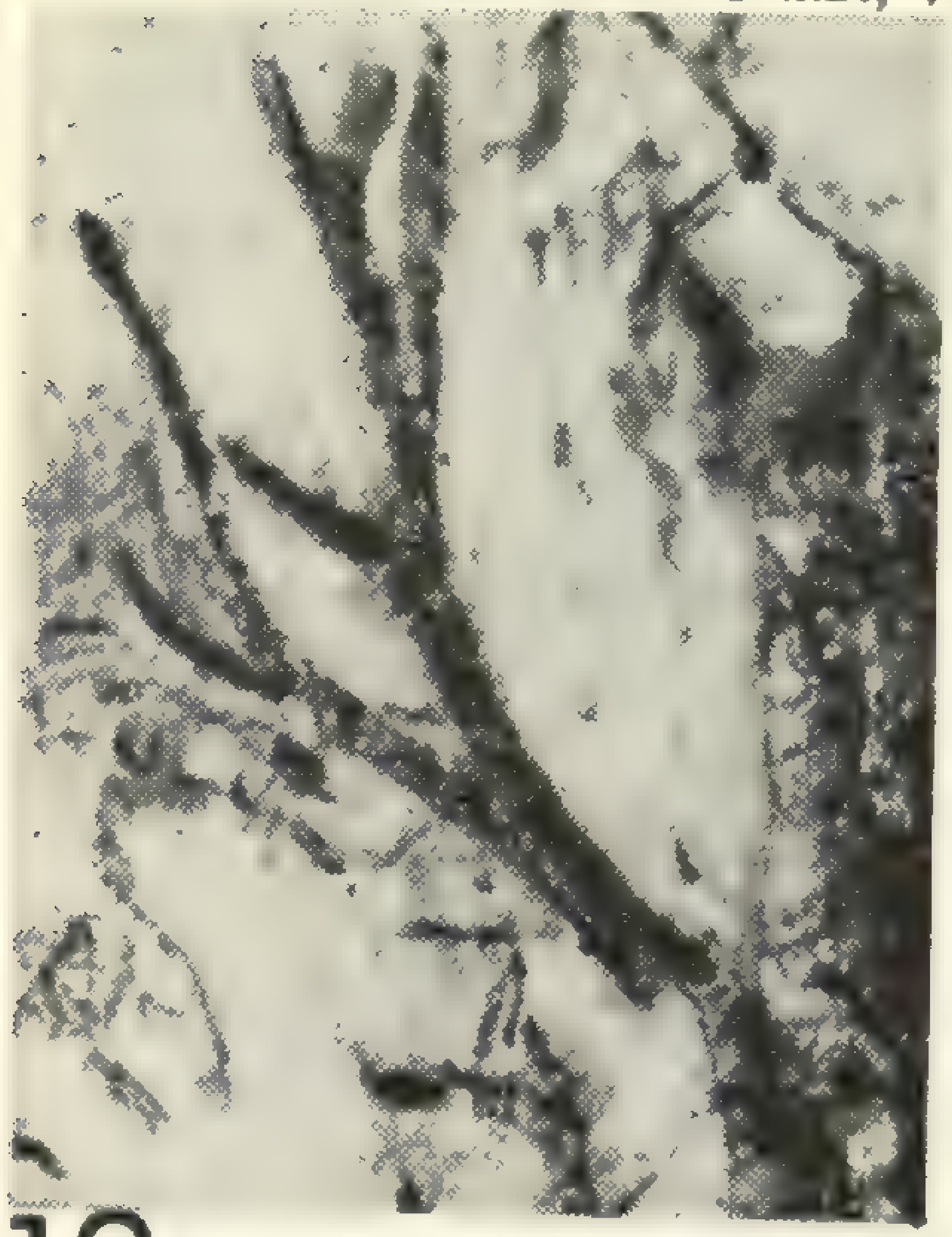
Fig. 15. Two leaves from specimen No. 5006, ×5, shown as they appeared originally. Fig. 16. Same leaves as in fig. 15 after degagement; portions distal to lines o----o were revealed after corresponding parts in fig. 15 were degaged away. These two leaves are shown on the right side of the extreme left branch of fig. 17. Fig. 17. Portion of specimen No. 5006, ×1. Fig. 18. Counterpart of specimen No. 5006, ×1.

Explanation of Plate

PLATE IV

Calamophyton bicephalum Leclercq and Andrews

Fig. 19. Leaf showing four orders of branching from specimen No. 5009/588, × 5. Fig. 20. Main stem of specimen No. 5011/609, ×1. Fig. 21. Holotype specimen No. 5011/609 shown natural size; figure 20 is counterpart of main stem shown here. Figs. 22–27 show stages in the excavation of a fertile appendage from specimen No. 5011/609; for explanation see text (p. 10); all ×5. Fig. 28. Portion of fertile appendage from specimen No. 5011/609, ×5.



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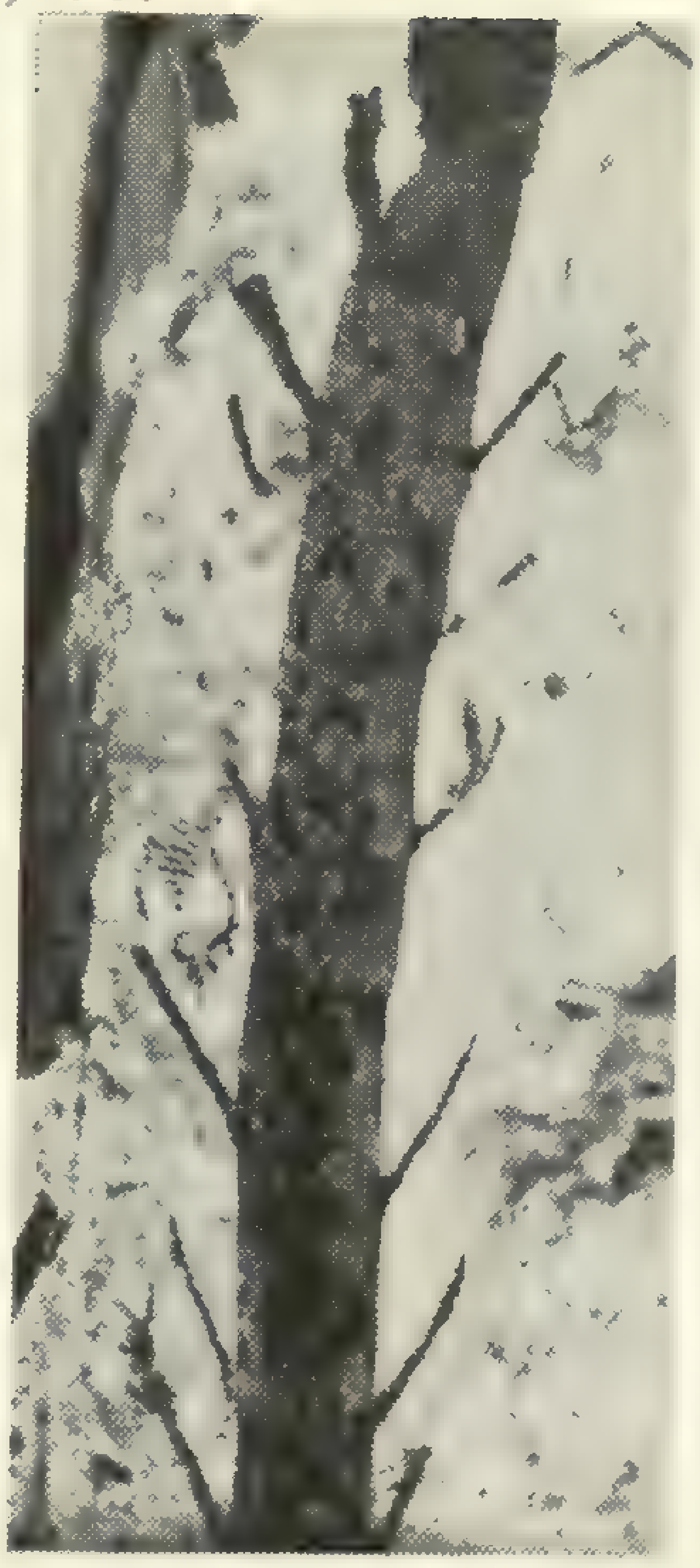

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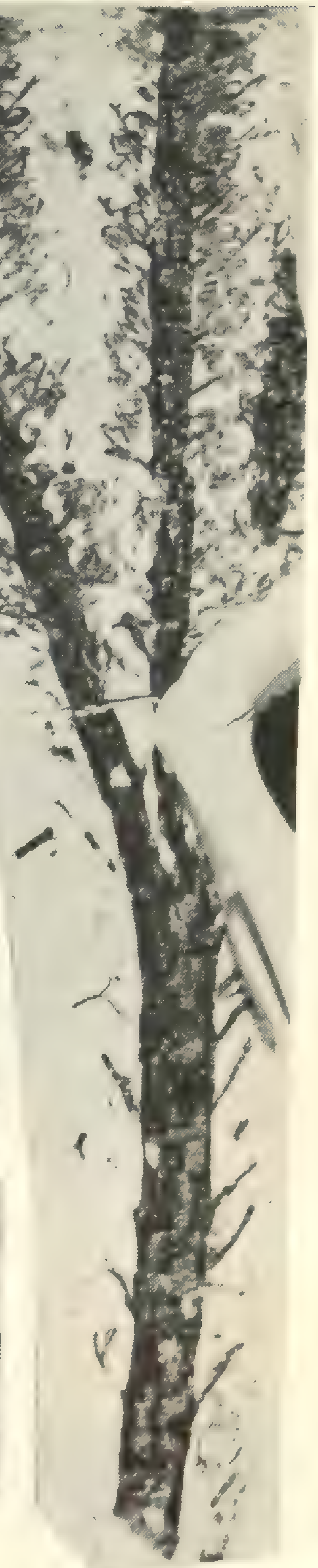

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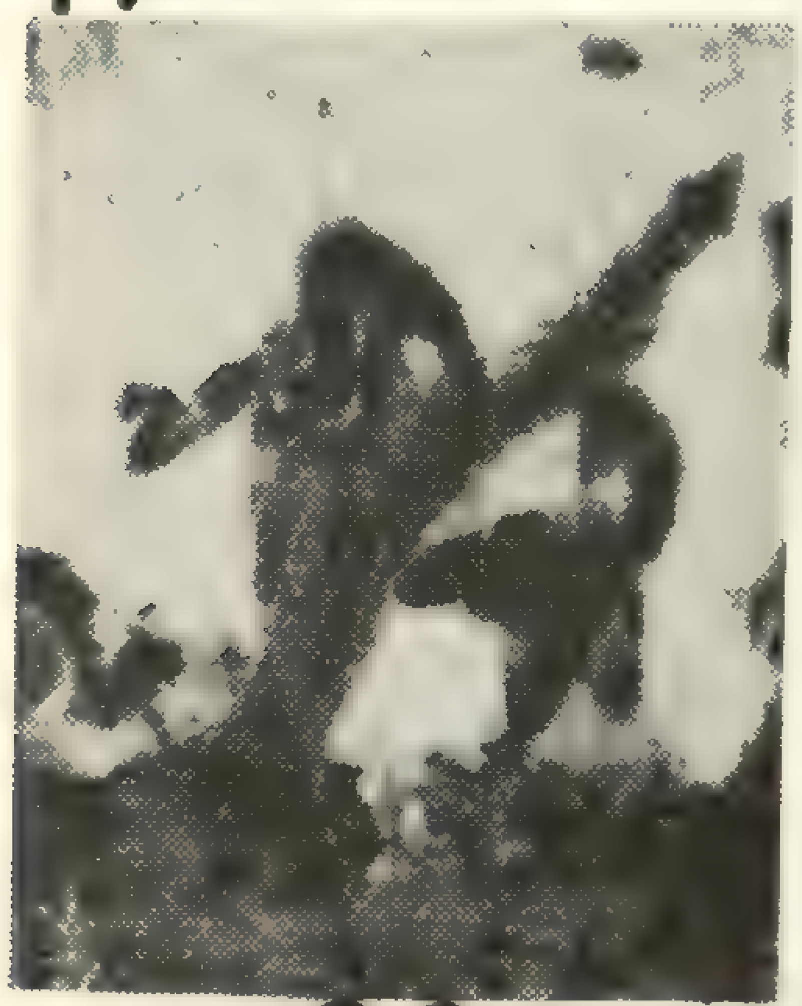

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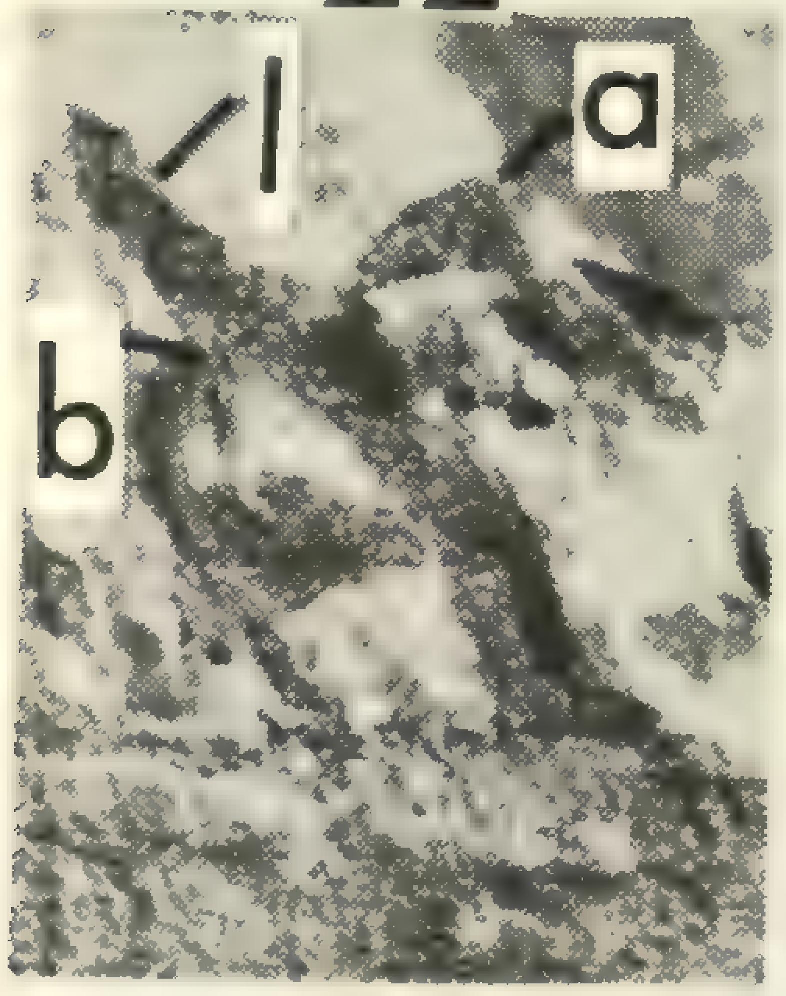

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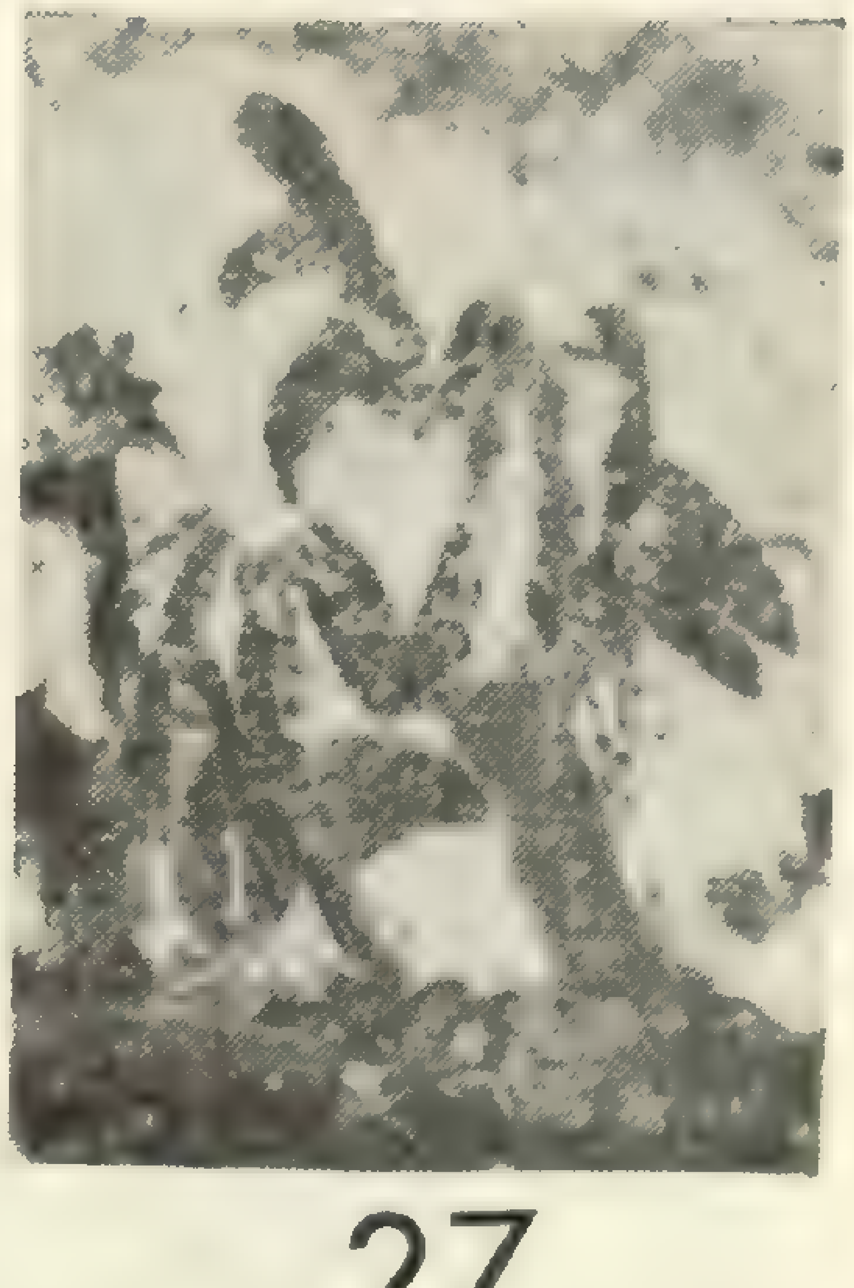

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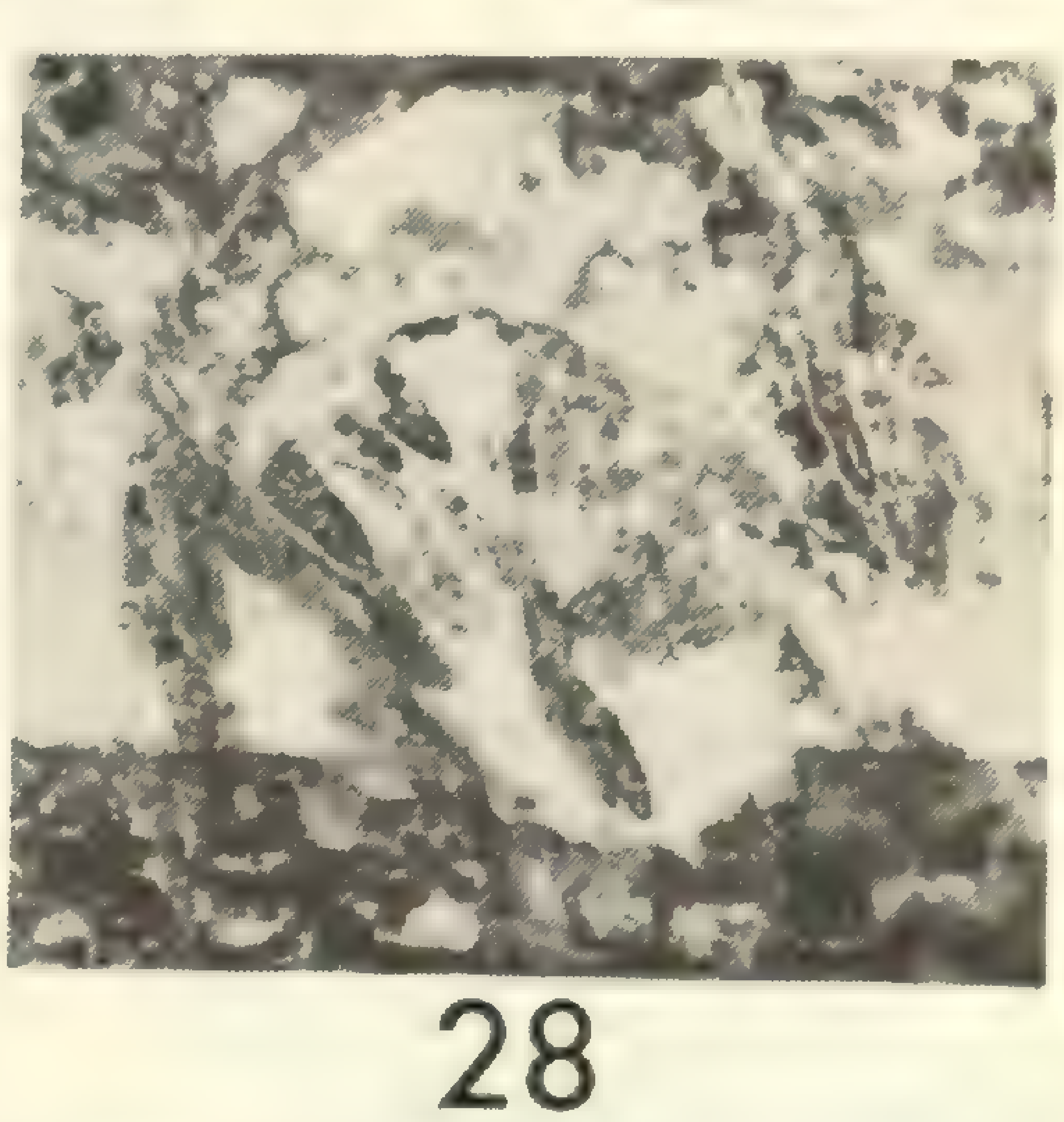

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LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

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LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM

Explanation of Plate

PLATE V

Calamophyton bicephalum Leclercq and Andrews

Fig. 29. Upper portion of holotype specimen No. 5011/609 (as shown in fig. 21) enlarged three times. Figs. 30, 31. Part and counterpart of a fertile appendage from specimen No. 5011/609, ×5; see also text figures 9–12 and description in text (p. 13).

CLASSIFICATION AND PHYLOGENY IN THE ORCHIDACEAE

ROBERT L. DRESSLER AND CALAWAY H. DODSON

ABSTRACT

The nomenclature of tribes and subtribes in the Orchidaceae is reviewed, and brought into line with the rules of botanical nomenclature. Tribal definition is discussed, and a different delineation of the Neottieae and Epidendreae is proposed. The Apostasieae are considered to be primitive orchids. The Vandeae are not considered to be clearly separable from the Epidendreae. A "phylogenetic" arrangement of recognized subtribes is proposed, and keys are given. A broader interpretation is given, especially of the subtribes Chloraeinae, Spiranthinae, Cyrtopodiinae, Epidendrinae, Maxillariinae and Oncidiinae. About 40 subtribes are recognized (as compared to 80 in Schlechter's system). The need for further revision is recognized. Evolutionary patterns are discussed for several features of the orchid plant, and the phylogeny of the family briefly considered. ROBERT L. DRESSLER, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri; CALAWAY H. DODSON, Instituto Botánico, Universidad de Guayaquil, Guayaquil, Ecuador.

INTRODUCTION

The Orchidaceae form one of the largest families of angiosperms, as well as one of the most fascinating by reason of their diversity and specialization in floral structure. A satisfactory classification of the orchids into tribes and subtribes is not yet available. The most commonly used system, that of Schlechter, has for some time not been in accord with the rules of nomenclature, and has many features which may be questioned on botanical grounds. The recent International Botanical Congress has clarified the rules concerning the nomenclature of categories between family and genus, and provides an occasion for a reevaluation of nomenclature in the Orchidaceae. In reviewing the groups within the Orchidaceae we have, of necessity, made a number of observations on relationships and probable phylogeny within the family. These form the final portion of this paper.

While many workers have described new genera and species of orchids, there has been very little monographic work, and we may safely say that the family has really been very little studied, considering its size and complexity. Until there has been a great deal more systematic study of the family it will not be possible to present a finished system of tribes and subtribes. Consequently, no new taxa are presented in this paper, but we have attempted only to review and evaluate previous systems of classification, and to present a tentative system, with synonymy.

Swartz, in 1880, first divided the orchids into those with a single fertile anther and those with two fertile anthers, thus providing the basis for the subfamilial divisions now recognized. Lindley, in his "Orchidearum sceletos" (1827), was the first to divide the family into tribes. In this work he recognized eight tribes. Later, in "The Genera and Species of Orchidaceous plants," only seven tribes were maintained, with "sections" or "divisions" recognized under some of these. Reichenbach never presented a detailed system of orchid classification, and his categories were vague and inconsistent in both rank and spelling (1852, 1884). Bentham (1881), in preparing a system for Genera Plantarum, recognized only five tribes, and delineated 27 subtribes under these. Pfitzer (1887) criticized the classification of Bentham and offered a revised system, based primarily on vegetative features. While the rank of Pfitzer's categories was not very clearly indicated,

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one finds that the groups with names ending in "-inae" are referred to as "Tribus." Thus Pfitzer's classification recognized 32 tribes, with a number of subtribes. This same system was followed in "Die Natürlichen Pflanzenfamilien," with only minor changes. Pfitzer's classification was the basis for Schlechter's posthumously published "System der Orchidaceen" (1926). Schlechter, however, recognized only four tribes and treated the remaining tribes and subtribes of Pfitzer all as subtribes, of which he enumerated eighty. Some of Schlechter's subtribes were characterized in earlier papers (1911, 1915) as "Gruppen," but only in the 1926 paper were they treated as subtribes. In studying Schlechter's work, one often feels that his system was published in unfinished form, and that he might have presented a much more coherent system, had he lived to complete it. Mansfeld (1937) has reviewed Schlechter's system and made some modifications, but most recent authors have followed Schlechter's original system with little change. Recently Hawkes and Heller (1959) have presented a list of subtribes and genera in which they recognize no less than 88 subtribes.

Schlechter might well be characterized as a "splitter"; he followed very narrow concepts at all levels of his classification. Subsequent workers have reduced a large proportion of his genera and species to synonymy, but most have accepted his tribes and subtribes with little question. Actually, many of the subtribal boundaries drawn by Schlechter have proven to separate closely related genera. In several cases genera assigned to different subtribes have proven interfertile. While Schlechter recognized eighty subtribes in the subfamily Orchidoideae and several others have since been proposed, we tentatively recognize only about forty in our proposed revision. We believe that future study may further reduce the number of subtribes to be recognized. While the rules of nomenclature permit an almost excessive number of categories between genus and species (subgenus, section, subsection, series and subseries), there are relatively few categories between family and genus. Where Schlechter's subtribes seem useful, even though too closely related or too poorly defined, we have indicated them as "alliances." These are not intended to have formal nomenclatural status. To recognize them as subtribes would tend too much toward taxonomic inflation, and would tend to obscure the really close relationships which exist within the family.

Some authors have cast doubt on the validity of genera which are interfertile. While we do not believe that a fertility criterion (alone) can be applied for generic status in the orchids, we do feel that interfertile genera should not be placed in separate subtribes. In every case where authentic hybrids have been reported between subtribes, however, the morphological evidence, alone, favors their union into a single group. In those cases where we feel quite sure that closely related genera were separated in Schlechter's system, we have united them into a single subtribe. In other cases, however, we have deferred judgment because of insufficient familiarity with the plants involved.

The main difference between Schlechter's system and our own is that he emphasized differences, while we are seeking resemblances. His system was primarily analytical and aimed at identification (though often faulty for that purpose), while our own is synthetic, as we believe these higher categories should be. This

is not to belittle the key features used by Schlechter. Where valid, these are still available for keying groups within the subtribes, but relationships are, we hope, more clearly shown in our system. In many cases the key features chosen by Schlechter will separate only a portion of the genera in closely related or artificial groups.

There are primarily three features of the International Code of Botanical Nomenclature which affect the choice or form of names used in this paper. In the case of subfamilies, tribes or subtribes, the name of any taxon which includes the type of the next higher taxon must be based on the same stem as the name of the next higher taxon. Thus "Ophrydeae" and "Platantherinae," for example, must be replaced by Orchideae and Orchidinae, respectively. This requirement, which was only recently added to the rules (by the 1959 Congress) causes a few changes, but should cause no confusion, and in general makes the taxonomy at this level more logical. The requirement of the suffixes *-oideae, -eae* and *-inae* for subfamilies, tribes and subtribes has been in the rules for some time, but has often been ignored by those dealing with orchid nomenclature. The same is true of the principle of priority, which demands the use of names proposed by Bentham, where these differ from those used by later workers.

Tribal Delineation

The separation and characterization of the tribes Apostasieae and Cypripedieae is relatively clear. Each forms a distinctive and natural group which is easily recognized. In the subfamily Orchidoideae the situation is rather different. The tribe Orchideae is distinctive and rather easily characterized, though clearly related to the Neottieae. The distinction of further tribes is much less clear. In Schlechter's system all of the genera with mealy or sectile pollen (except the Orchideae) are grouped in the tribe Polychondreae (= Neottieae), while the genera with hard, waxy pollinia are separated as the more advanced tribe Kerosphaerae (= Epidendreae). As Mansfeld has shown, the distinction between mealy and waxy pollinia is neither practical nor natural. Some genera of the Bletiinae have, according to Mansfeld, mealy pollinia. Certainly most of the remaining genera have rather soft pollinia. Some genera of the Sobraliinae have hard pollinia and this subtribe shows close affinity to the Thuniinae and the Epidendrinae. Similarly, the Arethusinae have mealy pollinia, but *Crybe* and *Jimensia* (*Bletilla*) are closely related to *Bletia.* There is a complete series ranging from free pollen grains to the hard ceraceous pollinia of the Oncidiinae and Sarcanthinae. Any arbitrary degree of cohesion chosen as a dividing line would split natural genera and subtribes. Mansfeld (1937) placed the Arethusinae and Sobraliinae in the Epidendreae, and this action is supported by the morphological studies of Hirmer (1920). Such a system, though, leaves no practical way of distinguishing the Epidendreae and Neottieae and is, we believe, still unnatural. The subtribes Vanillinae, Pogoniinae and Gastrodiinae seem to show much closer relationship to the Sobraliinae and Arethusinae than to the other subtribes of the Neottieae. By placing these subtribes in the Epidendreae one achieves a system which is both

more natural and more practical. By this arrangement the great majority of the primitive Epidendreae (with mealy pollinia) have incumbent, operculate anthers, like those of *Phajus* or *Cattleya* (see fig. 3D). The position of the anther in the more advanced Epidendreae is extremely diverse, but these are easily distinguished by the truly hard pollinia. A few species of primitive Epidendreae, such as *Triphora* and some species of *Epistephium* and *Elleanthus*, have erect anthers. Thus the position of the anther is not a fool-proof key feature, but it does seem to provide a better practical separation, as well as a more natural classification.

Several authors have distinguished the tribes Epidendreae and Vandeae on the basis of pollinia structure, but a clear distinction proves to be difficult. The presence or absence of a stipe is one feature which has been used for this purpose, but some genera which would unquestionably belong in the "Vandeae" have little or no stipe, while a few other genera which are not closely related have stipes or stipe-like structures (Genyorchidinae, Thecostelinae, some species of *Polystachya*). Another feature which is characteristic of the "Vandeae" is the presence of superposed pollinia; yet *Coelogyne* and some species of Thuniinae and *Polystachya* have more or less superposed pollinia, but seem otherwise not referable to the "Vandeae." There seems to be no feature or combination of features which will serve to separate the more advanced Orchidoideae into two clear-cut main groups. There is a general trend from plants with terminal inflorescence and relatively simple pollinia to those with a lateral inflorescence and highly specialized pollinia, but there is no sharp break and the relationships seem too reticulate to admit the separation of two tribes on this basis. The subtribes of the "Vandeae" (Cyrtopodiinae to Oncidiinae as listed on p. 29) seem to represent a relatively homogeneous and more specialized offshoot from some of the several evolutionary lines within the remainder of the Epidendreae. All of these subtribes appear to have been derived from more or less *Eulophia*-like ancestors. For this reason, it is sometimes convenient to consider them as a unit, and a better understanding of the subtribes related to the Cyrtopodiinae may indicate a sharper break between the two main divisions of the Epidendreae than is now evident.

While the Epidendreae form a natural and closely knit group, the Neottieae are more diverse in terms of relationship. Even with the removal of the Vanillinae, Pogoniinae and Gastrodiinae, it is not certain that the Neottieae form a really natural group. Including all of these genera in one tribe because they all possess mealy pollen is somewhat comparable to a hypothetical grouping of *Vanilla*, *Selenipedium*, and *Apostasia* into a single taxon because of seed characteristics. Mealy pollen, like the sclerotic seed coat and the lateral anthers of the Cypripedioideae, is a feature which was doubtless found in all orchids at an early stage in orchid evolution. Its occurrence in two or more otherwise dissimilar groups is scarcely strong evidence of relationship. Since the present paper is primarily a review of orchid classification, any major reorganization of the Neottieae or the Cypripedioideae must be deferred for the present. The possible groupings within these taxa are discussed in the final section on tribal phylogeny (p. 62).

Subfamily Cypripedioideae
- Tribe 1. Apostasieae
- Tribe 2. Cypripedieae

Subfamily Orchidoideae
- Tribe 3. Neottieae
  - Subtribe Limodorinae
  - Chloraeinae
  - Rhizanthellinae
  - Pterostylidinae
  - – – – – –
  - Neottiinae
  - – – – – –
  - Diuridinae
  - Cryptostylidinae
  - Prasophyllinae
  - – – – – –
  - Spiranthinae
    - a. *Tropidia* alliance
    - b. *Goodyera* alliance
    - c. *Spiranthes* alliance
    - d. *Cranichis* alliance
- Tribe 4. Orchideae
  - Subtribe Epipogiinae
  - Orchidinae
  - Disinae
    - a. *Disa* alliance
    - b. *Satyrium* alliance
  - Coryciinae
- Tribe 5. Epidendreae
  - Subtribe Vanillinae
  - Gastrodiinae
  - Pogoniinae
  - Sobraliinae
  - Thuniinae
  - Arethusinae
  - Bletiinae
  - Collabiinae

Tribe 5. Epidendreae (Continued)
  - Subtribe Coelogyninae
  - Epidendrinae
    - a. *Epidendrum* alliance
    - b. *Eria* alliance
    - c. *Polystachya* alliance
    - d. *Glomera* alliance
    - e. *Podochilus* alliance
    - f. *Arpophyllum* alliance
  - Pleurothallidinae
  - Adrorhizinae
  - Thelasiinae
  - Ridleyellinae
  - Liparidinae
  - Dendrobiinae
  - Genyorchidinae
  - Thecostelinae
  - – – – – –
  - Cyrtopodiinae
  - Catasetinae
  - Cymbidiinae
  - Sarcanthinae
  - Stanhopeinae
  - Maxillariinae
    - a. *Zygopetalum* alliance
    - b. *Lycaste* alliance
    - c. *Maxillaria* alliance
  - Pachyphyllinae
  - Cryptocentrinae
  - Oncidiinae
    - a. *Oncidium* alliance
    - b. *Ornithocephalus* alliance
    - c. *Dichaea* alliance
  - – – – – –

Subtribes of uncertain position
  - Grobyinae
  - Pachyplectrinae

A Proposed Phylogenetic List of Subtribes

Above is given a list of the tribes and subtribes which we recognize, followed by a tentative key to tribes. We have, in nearly all cases, changed the endings of the group names to accord with the rules of nomenclature. Very few of them were published in the appropriate form, though status was clearly indicated. We have attempted to arrange the groups in a "phylogenetic" sequence; that is, we

have tried to place the more primitive members at the beginning of each group, and we have tried to place closely allied groups together, where possible. The limitations of a one-dimensional scheme are obvious; there are, for example, a number of subtribes which should be immediately adjacent to the Epidendrinae in any "natural" system, but only two can be so placed. We have indicated groups of related subtribes by lines, but interrelationships within the Epidendreae are better shown in figure 1 (p. 51).

KEYS

As Schweinfurth has indicated (1959, p. 528), orchid identification has continued to be more of an art than a science. This is, in part, due to continued reliance on unworkable keys. Since previously published keys to the Orchidaceae have proven to be inadequate in many features, we have prepared these keys *de novo,* as much as possible. Comparison will show Schlechter's key to be much simpler in many respects. To this we can only reply, "Yes, but his key doesn't work." There will surely be many sections in these keys where a similar complaint is justified. It is extremely difficult to write a workable key to the orchids of the world. The person working in a single continent has an easier time of it, and would do well to prepare his keys independently, rather than trying to adapt either these or Schlechter's keys. An English translation of Schlechter's key, with some revision, is given in Withner's recent book (Schweinfurth, 1959).

KEY TO SUBFAMILIES AND TRIBES

1. Fertile anthers 2 or 3; filaments more or less united to the style, but arising below the level of the stigma; the stigma and terminal portion of the style free; no rostellum present........subfamily CYPRIPEDIOIDEAE........2
1. Fertile anther 1 (or 3 as an abnormality and in some autogamous forms); filaments united with the style to form a distinct column, united for the full length of the style *or* the anther and stigma connected by a terminal rostellum........subfamily ORCHIDOIDEAE........3
2(1). Perianth essentially regular, the lip never deeply saccate; fertile anthers 2 or 3, elongate; style slender........APOSTASIEAE
2. Perianth irregular, with a deeply saccate lip; fertile anthers 2, subglobose; a conspicuous, flattened median staminode present; style relatively thick........CYPRIPEDIEAE
3(1). Pollinia 2 to 8, hard, waxy; anther usually caducous; leaves various, often articulate; habit of growth various........EPIDENDREAE
3. Pollinia 2 or 4, soft, mealy, in tetrads or granular masses; anther persistent or deciduous; leaves usually herbaceous, not articulate; growth usually sympodial with a terminal inflorescence........4
4(3). Anther erect or reclinate (rarely incumbent), persistent, usually broadly joined to the column; pollinia in soft masses (sectile), caudicles arising from the base of the pollinia. ....ORCHIDEAE
4. Anther erect or incumbent, narrowly joined to the column, commonly caducous or withering; pollinia mealy or sectile, without caudicles or these indistinct and terminal........5
5(4). Anther terminal and operculate (incumbent) or rarely erect, usually more or less versatile; stems often with corms or corm-like thickenings........EPIDENDREAE
5. Anther more or less erect, often dorsal (terminal and operculate in some species of *Acianthus*); stems without corms or other thickenings........NEOTTIEAE

SYNONYMY AND DISCUSSION

In the following section we give keys to subtribes and list the subtribes alpha-

betically under the tribes, with synonymy and discussion where appropriate. We have not given full citations with the names of tribes and subtribes, but the papers containing new tribes or subtribes are indicated by an asterisk in the bibliography. We estimate that there are about 600 distinct, valid genera in the Orchidaceae. A really critical enumeration of genera is not yet possible. The lists given here are based primarily on Schlechter (1926), and doubtless contain some genera which do not merit recognition, while omitting others which should be listed. Only for the *Epidendrum* and *Oncidium* alliances can we indicate with some confidence the genera which will be maintained by critical revision; and, even here, there are genera of which we have not yet seen adequate or living material. If these alliances are representative of the family, the total number of valid genera may be well under 600.

Subfamily CYPRIPEDIOIDEAE Lindley (Diandrae Kunth, Pleonandrae Pfitzer [1903], Apostasioideae Wettstein)

Tribe 1. APOSTASIEAE R. Brown (Pulverae Blume, in part)

Some authors have excluded the Apostasieae as a separate family. We, however, agree with Rolfe (1909), J. J. Smith (1934), Mansfeld (1934) and Holttum (1953), that these plants cannot logically be excluded from the family without also excluding the Cypripedieae, and we feel that neither action is desirable. A classification which excludes the Apostasieae because they are inconspicuous and retains the Cypripedieae because they are showy is scarcely acceptable. It is possible, of course, that detailed study will show the Apostasieae to be basically different from other orchids in some features. As far as present knowledge goes, they are primitive orchids, and quite as closely related to some Neottieae as these are to the other orchids. As Godfery (1932) indicates, there is little evidence of close relationship between the Apostasieae and Cypripedieae, even though they show the same basic plan of flower structure. It is quite possible that the current subfamilial division is artificial.

Apostasia, Neuwiedia.

Tribe 2. CYPRIPEDIEAE

The four genera of ladyslippers form a relatively uniform relic group. They are markedly divergent from most other orchids in that the median anther is represented by a large shield-like staminode. In spite of their differences, the ladyslippers are orchids in good standing. The three abaxial stamens, resupination, reduction in seed structure, mycorrhizal relationship, and the less obvious features which predispose the family to evolution as epiphytes are themes which run throughout the family. The primitive features to be found in *Selenipedium* are strongly reminiscent of those found in other primitive orchids, though they do not, of course, necessarily indicate close relationship. Mansfeld (1937a) notes some resemblances between the Cypripedieae and *Epipactis.*

Cypripedium, Paphiopedilum, Phragmipedium, Selenipedium.

Subfamily ORCHIDOIDEAE (Monandrae Kunth)

Tribe 3. NEOTTIEAE Lindley (Granulosae Blume [in part], Pulverae Blume [in part], Goodyereae King & Pantling, Listereae King & Pantling, Polychondreae Schltr., Epipactieae Hatch [illigitimate, because nomenclaturally superfluous when published])

Key to Subtribes

1. Anther more or less terminal, erect or inclined, projecting beyond the stigma or rostellum; viscidium, if present, commonly attaching to the base or ventral surface of the pollinia, rarely to the apex.......2
1. Anther dorsal, not projecting beyond the erect rostellum; pollinia usually attached to a terminal viscidium.......6
2(1). Plants subterranean, or the flowers scarcely penetrating the surface of the soil; leafless saprophytes with the flowers in dense bracteate heads (Australia).......Rhizanthellinae
2. Plants appearing above the soil, usually forming leaves.......3
3(2). Rostellum sensitive, secreting a viscid drop when touched, or appearing to form a viscidium; small, slender-stemmed plants with 2 sub-opposite cauline leaves (leafless saprophytes in *Neottia*) (north temperate).......Neottiinae
3. Rostellum not sensitive, with or without a viscidium; leaves usually either several or basal.......4
4(3). Leaves cauline, spiral (absent in *Limodorum* and *Aphyllorchis*); lip usually divided into a basal, more or less saccate portion and a terminal, often hinged, portion (sub-entire and spurred in *Limodorum*); rostellum present or absent (largely north temperate).......Limodorinae
4. Leaves often basal; lip not as above; rostellum usually present.......5
5(4). Lip hinged, with a retrorse appendage at the hinge, actively motile (sensitive) (Australasia).......Pterostylidinae
5. Lip various, but not actively motile (South America and Australasia).......Chloraeinae
6(1). Column with distinct lateral wings or staminodia; plants with fascicled roots and basal leaves.......7
6. Column usually without distinct wings or staminodia; habit various.......9
7(6). Pollinia with a distinct caudicle-like stipe (Australasia).......Prasophyllinae
7. Pollinia without a stipe.......8
8(7). Staminodia very prominent, scarcely adnate to the style; column not more or less hidden by the enfolding lip base; sepals or petals relatively broad (Australasia).......Diuridinae
8. Staminodia relatively small; column very short, nearly hidden by the base of the lip; both sepals and petals very narrow (Australasia).......Cryptostylidinae
9(6). Rostellum sensitive, secreting a viscid drop when touched, or appearing to form a viscidium; small, slender-stemmed plants with 2 subopposite cauline leaves (leafless saprophytes in *Neottia*) (north temperate).......Neottiinae
9. Rostellum not sensitive, usually with a distinct viscidium; habit not as above (widespread).......Spiranthinae

Chloraeinae Pfitzer (Caladeniinae Pfitzer, Thelymitrinae Pfitzer, Acianthinae Schltr., Corysanthinae Schltr., Megastylidinae Schltr., Corybasinae Mansf. [not validly published, unless later (1954) reference to Corysanthinae Schltr. be taken to validate its publication as a new name. Corysanthinae, however, is a valid name, though based on a synonym])

This is the group which includes most of the bizarre Australian genera. The striking modifications have led to the naming of several subtribes, but these do not seem tenable, at least as previously delimited. *Thelymitra* is distinctive because of its nearly regular perianth, which is frequently blue, but it is closely allied to the

other genera through *Calochilus, Adenochilus* and *Glossodia.* Some species of *Thelymitra* are unusual for this group in the attachment of the rostellum or viscidium to the apex of the pollinia, but this is not consistent within the genus. Some species of *Acianthus* are very unusual in the form of the column and the position of the anther (operculate), but *A. reniformis* is more representative of the subtribe in these features; Mansfeld's action in grouping *Acianthus* with *Caladenia,* thus seems correct. *Corybas* is closely related to *Caladenia.* The three American genera *Chloraea, Bipinnula* and *Asarca* are somewhat distinctive in habit, but the other American genus, *Codonorchis,* is closely related to both *Chloraea* and *Caladenia.* Most of the Australian genera show a characteristic pitted, conic anther.

Acianthus, Adenochilus, Asarca, Bipinnula, Burnettia, Caladenia, Calochilus, Chiloglottis, Chloraea, Codonorchis, Corybas, Epiblema, Eriochilus, Glossodia, Leptoceras, Lyperanthus, Megastylis, Rimacola, Thelymitra, Townsonia.

CRYPTOSTYLIDINAE Schltr.

Cryptostylis is a distinctive genus, though without striking key features. Some species mimic insects and are involved in the strange relationship of pseudocopulation. This subtribe, the Diuridinae and the Prasophyllinae seem to form a distinct group with column structure similar to that of the Spiranthinae. The degree of relationship to the Spiranthinae is uncertain.

Coilochilus, Cryptostylis.

DIURIDINAE Bentham

This group is of special morphological interest because of the large staminodia and because the filament and style are scarcely united into a column. Some Spiranthinae show similar columnar structure, though without the staminodia.

Diuris, Orthoceras.

LIMODORINAE Bentham (Cephalantherinae Pfitzer, Epipactiinae Godfery)

The Limodorinae include genera which are quite primitive in some respects, and, being largely European, they have been studied much more than other primitive orchids.

Aphyllorchis, Cephalanthera, Epipactis, Limodorum.

NEOTTIINAE (Listerinae Schltr.)

These genera are distinctive in the sensitive rostellum, which forcibly extrudes a viscid droplet when touched. The anther is either erect or somewhat incumbent on the subequal rostellum. These genera show some resemblances to the Limodorinae, and, like that group, have relatively large chromosomes (Duncan, 1959).

Listera, Neottia.

PRASOPHYLLINAE Schltr.

Mansfeld placed these genera with *Thelymitra,* but they are distinctive in aspect, and unusual in the possession of stipes. These are generally described as

caudicles, but are not derived from the pollinia (see Vermeulen, 1959). This group seems more nearly allied to the Diuridinae and Cryptostylidinae.

Corunastylis, Goadbyella, Microtis, Prasophyllum.

PTEROSTYLIDINAE Pfitzer (Drakaeinae Schltr.)

These Australian genera are remarkable for their sensitive, motile lip, but very closely allied to the Chloraeinae, and especially to *Chiloglottis.*

Caleana, Drakaea, Pterostylis, Spiculaea.

RHIZANTHELLINAE Rogers

Rogers placed this group near the Gastrodiinae, but the form of the lip, column and anther indicate that they are allied to *Caladenia.*

Cryptanthemis, Rhizanthella.

SPIRANTHINAE Bentham (Corymbidinae Bentham [based on *Corymbis,* an orthographic variant of *Corymborchis*], Cranichidinae Pfitzer, Physurinae Pfitzer [based on *Physurus* L. C. Rich., nom. nud.], Tropidiinae Pfitzer, Maniellinae Schltr.)

We feel confident that the Spiranthinae and Cranichidinae should be merged. These groups have much the same floral structure, and we see little justification for separating them, especially if some American authors are correct in reducing Schlechter's Spiranthinae nearly to a single genus. The genera included in the *Goodyera* alliance are somewhat distinct in habit (rooting at the nodes, rather than roots fascicled), but agree well in floral features. Here, too, there seem to be too many genera. If future study should indicate the advisability of segregating the group as a separate subtribe, the name might be based on the familiar genus *Goodyera.* The *Tropidia* alliance seems to have the strongest claim to subtribal distinction, but no differences in floral structure have been demonstrated. In habit, these genera resemble *Palmorchis,* of the Sobraliinae, and *Apostasia.* The earliest subtribal name, Corymbidinae, should be changed in form, if it is to be used.

KEY TO ALLIANCES

1. Stem hard, woody; leaves subcoriaceous, strongly plicate, with several prominent nerves beneath (widespread) .... *Tropidia* alliance
1. Stem and leaves herbaceous, leaves not strongly plicate 2
2 (1). Roots not fascicled, scattered along the stem or rhizome; pollinia often sectile (widespread) .... *Goodyera* alliance
2. Roots usually fascicled; pollinia not sectile 3
3 (2). Flower resupinate, lip lowermost (widespread, but predominantly American) .... *Spiranthes* alliance
3. Flower not resupinate, lip uppermost (American) .... *Cranichis* alliance

a. GOODYERA ALLIANCE: *Anoectochilus, Cheirostylis, Cystopus, Cystorchis, Dicerostylis, Dossinia, Erythrodes (Physurus), Eucosia, Eurycentrum, Gonatostylis, Goodyera, Gymnochilus, Haemaria, Herpysma, Hetaeria, Hylophila, Kuhlhasseltia, Lepidogyne, Macodes, Moerenhoutia, Myrmechis, Odontochilus, Orchipedum, Papuaea, Platylepis, Tubilabium, Vrydagzynea, Zeuxine.*

b. CRANICHIS ALLIANCE: *Altensteinia, Baskervillea, Cranichis, Fuertesiella, Pontheiva, Porphyrostachys, Prescottia, Pseudocentrum, Pterichis, Solenocentrum, Stenoptera, Wullschlaegelia.*

c. SPIRANTHES ALLIANCE: *Centrogenium, Eurystyles, Lankesterella, Manniella, Pelexia, Sarcoglottis, Sauroglossum, Spiranthes.*

d. TROPIDIA ALLIANCE: *Corymborchis, Tropidia.*

Tribe 4. ORCHIDEAE (Granulosae Blume. [in part], Ophrydeae Lindley, Epipogieae Parlatore)

Here, except for the inclusion of the Epipogiinae in this tribe, we have followed essentially the classification of Bentham, which seems to be the best. There are still several problems in the morphological interpretation of flower structure in the Orchideae. Until this is better understood, it is difficult to consider the evolution or relationships of the group. As Godfery (1933) and Swamy (1949) have indicated, the Orchideae are clearly more highly specialized than the majority of Neottieae, and should not precede them in a phylogenetic scheme.

KEY TO SUBTRIBES

1. Lip erect, adnate to the face of the column, commonly bearing an appendage which overtops the anther; dorsal sepal and petals commonly forming a hood (Old World). .... CORYCIINAE
1. Lip free from the column 2
2(1). Leafless saprophytes; the anther erect or incumbent, narrowly attached to the column (Old World) .... EPIPOGIINAE
2. Autophytes with green leaves (except for *Silvorchis*); the anther erect or reclinate, broadly attached to the column 3
3(2). Anther erect or suberect, not projecting dorsally from the column; stigma simple or often divided into 2 separate, often stipitate, lobes; spur, if present, single and formed by lip (widespread) .... ORCHIDINAE
3. Anther more or less reclinate, projecting dorsally from the column, or recumbent, with the base uppermost, rarely suberect; stigma not divided into two completely separate lobes; median sepal sometimes spurred (Old World, predominantly African). .... DISINAE

CORYCIINAE Bentham (Disperidinae Schltr.)

Ceratandra, Corycium, Disperis, Pterygodium.

DISINAE Bentham (Satyriinae Pfitzer)

These genera seem better treated as a single subtribe. The position of the saprophytic *Silvorchis* is uncertain.

KEY TO ALLIANCES

1. Flowers resupinate; spur, when present, formed by median sepal; column relatively short (Africa) .... *Disa* alliance
1. Flowers not resupinate; spur or spurs, when present, formed by lip; column usually elongate (Old World) .... *Satyrium* alliance

a. DISA ALLIANCE: *Brownleea, Disa, Schizodium.*

b. SATYRIUM ALLIANCE: *Pachites, Satyrium, Silvorchis*?

EPIPOGIINAE Schltr.

Recent authors have placed these genera in the Neottieae, but the persistent anther and the sectile pollinia with basal caudicles indicate a much closer affinity with the Orchideae. Godfery (1933) followed Parlatore (1858) in treating

Epipogium as the type of a separate tribe. In *Epipogium aphyllum* the anther is incumbent and the pollinia are parallel with the caudicles, which attach to a viscidium near the apices of the pollinia. It is not clear that the incumbent anther indicates a relationship with the primitive Epidendreae; the peculiar orientation of the caudicles suggests that it is a derived condition in this species. Rohrbach (1866) gives detailed illustrations of *E. aphyllum.* The anther is erect in the autogamous *E. roseum* (as it is in the young bud of *E. aphyllum*) and the caudicles are apparently functionless. The detailed structure of *Stereosandra* is not well known, but the anther is erect and the pollinia bear caudicles. These genera probably are not very closely related to the Gastrodiinae, though, being saprophytes, they are superficially similar.

Epipogium, Stereosandra.

Orchidinae (Angiadeniae Parlatore, Habenariinae Bentham, Serapiadinae Bentham, Ophrydinae Bentham & Hooker, Gymnadeniinae Pfitzer, Androcorydinae Schltr., Huttonaeinae Schltr., Platantherinae Schltr.)

The union of the Platantherinae and Habenariinae of Schlechter is certainly appropriate, when there is yet disagreement as to whether or not *Habenaria* and *Platanthera* are distinct genera. This group is seriously in need of monographic attention. The extreme "splitting" of European workers combined with the (equally unrealistic) extreme "lumping" of recent American workers has led to taxonomic chaos.

Aceratorchis, Aceras, Acrostylia, Amitostigma, Anacamptis, Androcorys, Arnottia, Bartholina, Benthamia, Bicornella, Bonatea, Brachycorythis, Centrostigma, Chamaeorchis, Coeloglossum, Cynorchis, Dactylorchis, Deroemera, Diphylax, Diplacorchis, Diplomeris, Dithrix, Galeorchis, Gennaria, Gyaladenia, Gymnadenia, Habenaria, Herminium, Himantoglossum, Holothrix, Huttonaea, Leucorchis, Loroglossum, Neobolusia, Neotinea, Neottianthe, Nigritella, Ophrys, Orchis, Peristylus, Perularia, Phyllomphax, Platanthera, Platycoryne, Roeperorchis, Schizochilus, Schwartzkopffia, Serapias, Stenoglottis, Steveniella, Traunsteinera, Tylostigma.

Tribe 5. EPIDENDREAE Lindley (Cereaceae Blume, Arethuseae Lindley, Gastrodieae Lindley, Malaxideae Lindley, Vandeae Lindley, Kerosphaerae Schltr., all but 4 of Pfitzer's 31 tribes [1887], Sturmieae Pfitzer [1897]).

Key to Subtribes

1.	Growth sympodial, each shoot of limited growth and followed by other shoots from (usually basal) axillary buds (except *Vanilla* and *Galeola,* which are fleshy vines)	2
1.	Growth monopodial, the inflorescence axillary and the stem usually growing indefinitely in length	38
2 (1).	Pollinia soft, mealy	3
2.	Pollinia in compact masses, more or less hard, waxy in texture	7
3 (2).	Sepals and petals more or less united (except in *Stigmatodactylus*); flowers often tubular; plants saprophytic (widespread)	Gastrodiinae
3.	Sepals and petals not united; plants autophytes or saprophytes	4
4 (3).	Plants with corms; stems short; leaves narrow and grass-like (North America and temperate Asia)	Arethusinae
4.	Plants without corms (except in *Nervilia*), stems elongate; leaves various	5
5 (4).	Leaves articulated at the base, deciduous (America and Africa)	Sobraliinae
5.	Leaves not articulated, persistent	6

6(5). Seed with wing or sclerotic testa; fleshy vines, or sub-shrubs with a distinct calyculus below the ovary (widespread)........ VANILLINAE
6. Seed without wing or sclerotic testa, seed coat thin and reticulate; plants not as above (widespread)........ POGONIINAE
7(2). Inflorescence terminal or upper axillary, occasionally on young shoots before leaves develop (lateral and basal in a few species of *Epidendrum*, *Dendrobium*, *Coelogyne* and *Pleurothallis*)........ 8
7. Inflorescence lateral, usually basal........ 25
8(7). Leaves plicate........ 9
8. Leaves conduplicate........ 16
9(8). Flowers borne on separate leafless shoots which alternate with the unifoliate vegetative shoots (Asia)........ COLLABIINAE
9. Flowers and foliage borne on same shoot........ 10
10(9). The pollinia naked, without caudicles (see also *Pseuderia*, Dendrobiinae) (widespread). .... LIPARIDINAE
10. The pollinia bearing caudicles........ 11
11(10). Pollinia 8........ 12
11. Pollinia 2 or 4........ 13
12(11). Flower with a distinct column foot and mentum (Asia, *Eria* alliance)........ EPIDENDRINAE
12. Flower without a column foot or mentum (America and Africa)........ SOBRALIINAE
13(11). Pseudobulbs or corms of a single internode; pollinia 4, usually without a viscidium (Asia)........ COELOGYNINAE
13. Pseudobulbs or corms, if present, usually of several internodes........ 14
14(13). Stems usually forming either corms or pseudobulbs; rostellum with a distinct viscidium (widespread)........ CYRTOPODIINAE
14. Stems elongate, not forming corms or pseudobulbs; viscidium present or absent........ 15
15(14). Plants Asiatic, usually with large, showy flowers........ THUNIINAE
15. Plants American, with small, inconspicuous flowers (*Palmorchis*)........ SOBRALIINAE
16(8). Pollinia 2, 4, 6 or 8, clavate or laterally flattened........ 17
16. Pollinia 2 and semi-globose or 4 and superposed........ 22
17(16). Asiatic plants with elongate stems and terminal inflorescence of large showy flowers; pollinia 8........ THUNIINAE
17. Not with the above *combination* of features........ 18
18(17). The ovary articulated to the pedicel, the pedicel persisting; pollinia clavate; plants without pseudobulbs (America)........ PLEUROTHALLIDINAE
18. The ovary not articulated to the pedicel, the pedicel falling with the flower........ 19
19(18). Pollinia naked, without caudicles (rarely with viscidium)........ 20
19. Pollinia with caudicles........ 21
20(19). Flowers with a distinct column foot and mentum (except in *Pseuderia*) (widespread, predominantly Asiatic)........ DENDROBIINAE
20. Flowers without a column foot or mentum (widespread)........ LIPARIDINAE
21(19). Clinandrium more or less petaloid, overtopping the anther; pollinia 4; pseudobulbs of a single internode; inflorescence terminal (Asia)........ COELOGYNINAE
21. Clinandrum usually not petaloid nor overtopping the anther; pollinia 2–8; pseudobulbs usually of several internodes; inflorescence often upper axillary (widespread). .... EPIDENDRINAE
22(16). Plants with pseudobulbs........ 23
22. Plants without pseudobulbs, stems elongate........ 24
23(22). Pseudobulbs of a single internode; clinandrium petaloid and overtopping the anther; pollinia without a viscidium (Asia)........ COELOGYNINAE
23. Pseudobulbs of several internodes; clinandrium not petaloid, nor overtopping anther, pollinia with a viscidium (*Polystachya*, largely African)........ EPIDENDRINAE
24(22). Lip free from the column; flowers large (Asia)........ THUNIINAE
24. Lip completely adnate to the column; flowers very small (*Epidanthus*, America). .... EPIDENDRINAE
25(7). Leaves plicate........ 26
25. Leaves conduplicate........ 30

26(25). Pseudobulbs or corms of several internodes, when present.......27

26. Pseudobulbs usually of a single internode (rarely absent in the *Zygopetalum* alliance). 29

27(26). Pollinia 4 or (usually) 8, clavate or laterally flattened, without stipe and usually without viscidium (widespread).......BLETIINAE

27. Pollinia 2, or 4 and superposed, with a distinct viscidium and usually with a stipe.......28

28(27). Pollinia 2 or 4; plants usually with corms, sometimes with elongate pseudobulbs and basal inflorescence; lip often hinged or spurred (widespread).......CYRTOPODIINAE

28. Pollinia 4; plants with elongate pseudobulbs; inflorescences usually lateral on the pseudobulb; lip often saccate, but neither hinged nor spurred; anther usually sensitive, forcibly expelling the pollinia when triggered (America).......CATASETINAE

29(26). Lip immobile, often with antenna-like processes; flowers usually racemose (America). .......STANHOPEINAE

29. Lip usually hinged at base and mobile, without antenna-like processes; flowers often solitary (America).......MAXILLARIINAE

30(25). Pollinia 2–8 (usually 4), clavate or laterally flattened, often without caudicle or stipe.......31

30. Pollinia 2, or 4 and superposed, usually with stipe and viscidium.......36

31(30). Pollinia naked, without caudicles, usually without a viscidium, never with stipe or caudicles.......32

31. Pollinia not naked, usually with distinct viscidium and stipe or caudicles.......33

32(31). Pollinia 2 or 4; inflorescence various (widespread, predominantly Old World)....... .......DENDROBIINAE

32. Pollinia 8; inflorescence paniculate (New Guinea).......RIDLEYELLINAE

33(31). Flower with a pronounced column foot; stipe present, frequently double.......34

33. Column foot slight or absent; no true stipe present.......35

34(33). Lip and base of column more or less united into a tubular structure (Asia)....... .......THECOSTELINAE

34. Lip free from column, not forming a tubular structure (Old World).....GENYORCHIDINAE

35(33). Pollinia 4, the caudicles inconspicuous; roots extremely thick (Ceylon and South India).......ADRORHIZINAE

35. Pollinia 8, with a long caudicle; roots not especially thick (Asia).......THELASIINAE

36(30). Pseudobulbs usually of several internodes (Old World).......CYMBIDIINAE

36. Pseudobulbs of a single internode.......37

37(36). Lip usually hinged to the base of the column, mobile; flowers usually solitary; often with a wide semilunate viscidium and short indistinct stipe (America).......MAXILLARIINAE

37. Lip not hinged to the base of the column, immobile; viscidium usually compact, clearly differentiated from the stipe (America).......ONCIDIINAE

38(1). Clinandrium petaloid, overtopping anther; small American plants.......PACHYPHYLLINAE

38. Clinandrium not petaloid, not overtopping the anther.......39

39(38). Old World plants.......40

39. American plants.......41

40(39). Pollinia 8, without a stipe (but with a long caudicle).......THELASIINAE

40. Pollinia 2 or 4, with a distinct stipe (see also *Dipodium*, Cymbidiinae).......SARCANTHINAE

41(39). Flower with a distinct spur.......42

41. Flowers without spurs (except in *Rodriguezia*, Oncidiinae).......43

42(41). Flowers in racemes, *or* plants leafless; spur not concealed by a bract.......SARCANTHINAE

42. Flowers solitary; spur parallel with the pedicel and usually concealed by a bract; plants leafy.......CRYPTOCENTRINAE

43(41). Lip hinged to the base of the column, mobile; flowers usually solitary, often with a wide semilunate viscidium and a short indistinct stipe.......MAXILLARIINAE

43. Lip not hinged to the base of the column, immobile; viscidium usually compact, clearly differentiated from the stipe.......ONCIDIINAE

ADRORHIZINAE Schltr.

Schlechter placed this group near the Coelogyninae, while Kränzlin allied them to *Dendrobium* or *Eria.* These views are not necessarily opposed, as we believe the Coelogyninae and Epidendrinae (esp. *Eria*) to be closely related. These genera appear to be closest to *Eria,* but are distinguished by the lateral inflorescence and fewer pollinia.

Adrorhizon, Josephia.

ARETHUSINAE Bentham (Bletillinae Schltr.)

These largely north temperate genera have corms or fleshy rhizomes and closely resemble the Bletiinae, but the pollinia are mealy and without caudicles. *Crybe* and *Jimensia* may well be more closely related to *Bletia* than to *Arethusa.*

Arethusa, Calopogon, Crybe, Jimensia (Bletilla).

BLETIINAE Bentham (Chysiinae Schltr., Phajinae Schltr.)

Chysis is apparently allied to *Acanthephippium. Coelia* and *Bothriochilus* are placed here on the subplicate leaves, the lateral inflorescence and the relatively soft, subclavate pollinia. They do not show close relationship to the genera of the Epidendrinae. *Basiphyllaea,* similarly, is out of place among the Epidendrinae; it seems to differ from *Bletia* primarily in size. *Hexalectris* is closely allied to *Bletia,* and less so to *Chysis. Bletia* closely resembles some species of *Laelia* (Epidendrinae) in flower structure, and these genera may be more closely related than is indicated by our present classification.

Acanthephippium, Ancistrochilus, Anthogonium, Ascotaenia, Aulostylis, Basiphyllaea, Bletia, Bothriochilus, Calanthe, Chysis, Coelia, Gastorchis, Hexalectris, Ipsea, Pachystoma, Phajus, Plocoglottis, Spathoglottis, Taeniopsis.

CATASETINAE Schltr.

This is an interesting group because of the usually sensitive anther, but some species of *Catasetum* (or *Clowesia*) lack this feature. These genera are apparently related to the Cyrtopodiinae (especially *Cyrtopodium* and *Galeandra*).

Catasetum, Cycnoches, Mormodes.

COELOGYNINAE Bentham

The flower structure of this group is close to that of the Epidendrinae and Bletiinae, but the habit is distinctive, and the pollinia are superposed in some genera.

Acoridium, Basigyne, Bulleyia, Coelogyne, Dendrochilum, Dickasonia, Gynoglottis, Ischnogyne, Nabaluia, Neogyne, Otochilus, Panisea, Pholidota, Pleione, Pseudacoridium, Sigmatogyne.

COLLABIINAE Schltr.

These genera seem to be very closely allied to both the Bletiinae and the Cyrtopodiinae. *Tainia* and *Nephelaphyllum* are certainly allied to *Eulophia.* The

habit of this group is relatively distinctive, while the structure of the pollinia is somewhat diverse.

Chrysoglossum, Collabium, Diglyphosa, Hancockia, Mischobulbon, Nephelaphyllum, Pilophyllum, Tainia.

Cryptocentrinae Garay

These genera were placed in the Maxillariinae by Schlechter, apparently because of the habit and 1-flowered inflorescence. Schlechter considered *Sepalosaccus* (which we have not seen) to be intermediate between *Maxillaria* and *Cryptocentrum.* Garay has created a separate subtribe for *Cryptocentrum,* on the basis of the conspicuous spur (other features listed by Garay are present in the *Maxillaria* alliance or are different aspects of the spur). According to Garay, *Cryptocentrum* would find its closest affinity in the Oncidiinae, but we are unable to agree with this conclusion. We believe that the genus most closely approaches *Trigonidium* (Maxillariinae). *Cryptocentrum* is usually monopodial, but sympodial species occur. The genus is rather distinctive and may merit a separate subtribe, but further study is needed.

Anthosiphon, Cryptocentrum.

Cymbidiinae Bentham

The Cymbidiinae bear a general resemblance to the Bletiinae, but seem to be distinct in both habit and structure of pollinia. A single hybrid between *Phajus* and *Cymbidium* is recorded. Rolfe (1911) has shown that this parentage is probably in error. Many more recent attempts to cross these genera have failed. *Ansellia* closely resembles *Grammatophyllum* and, like that genus, has conduplicate leaves and sometimes bears lateral inflorescences (while *Grammatophyllum* may rarely produce a terminal inflorescence). *Ansellia* must be placed in the Cymbidiinae, if this group can be maintained separate from the Cyrtopodiinae. Perrier (1941) assigns *Grammangis* and *Cymbidiella* to the Cyrtopodiinae and suggests that the two groups cannot be separated. The Cymbidiinae generally have elongate stems or pseudobulbs with several or many leaves, while the few Cyrtopodiinae which have conduplicate leaves usually have very short, unifoliate pseudobulbs, but this is surely not a very convincing separation; further study is needed. Holttum (1958) indicates the probable relationships of this subtribe to the Sarcanthinae, from which a few monopodial species are not easily distinguished by any "key" feature. *Acriopsis* resembles *Porphyroglottis,* but is unusual in the petaloid clinandrium, the union of the lip and column, and the form of the pollinia. It may deserve a separate subtribe, but it is not closely allied to *Thecostele.*

Acriopsis?, Ansellia, Caloglossum, Cymbidiella, Cymbidium, Cyperorchis, Dipodium, Grammangis, Grammatophyllum, Poicilanthe, Porphyroglottis.

Cyrtopodiinae Bentham (Eulophiinae Bentham, Corallorhizinae Schltr., Calypsoinae Schltr., Eulophidiinae Schltr.)

Several of these genera were placed in the Polystachyinae by Schlechter, but they show little affinity to *Polystachya,* and are separated from the Cyrtopodiinae only by the position of the inflorescence. The peculiar anther of *Galeandra* is duplicated

in some species of *Eulophia* (and among the Collabiinae). *Corallorhiza* is clearly allied to *Oreorchis* and *Aplectrum*. While brought together from diverse parts of Schlechter's system, this forms one of the more natural subtribes. It is usually characterized by corms (rhizomes in the saprophytes, pseudobulbs in some species of *Galeandra*, *Eulophia* and *Cyrtopodium*), plicate leaves and 2 or 4 (superposed) pollinia with a distinct viscid disk, but little or no stipe. The lip and column of *Calypso* are distinctive, but it is apparently related to *Dactylostalix* and *Yoania*, which are more characteristic of the subtribe. For the placement of *Yoania* in this group, see Finet (1896). *Cyrtopodium* is somewhat distinctive in habit and the form of the lip, but the habit is approached by some species of *Eulophia* and *Galeandra*. Schlechter's inclusion of *Eulophia* in the Cyrtopodiinae would seem to require the use of this name, rather than Eulophiinae, for this group.

Schlechter assigns *Eulophidium* to a separate subtribe, but Mansfeld places it in the Cyrtopodiinae. Perrier (1941) goes so far as to treat *Eulophidium* as a subgenus of *Lissochilus*. The American species are distinctive in habit and closely resemble *Oncidium* section *Miltoniastrum*. This section of *Oncidium* has relatively simple rostellar structure, and it is possible that *Eulophidium* represents a phyletic link between the Cyrtopodiinae and the Oncidiinae.

Acrolophia, Calypso, Corallorhiza, Cremastra, Cyanaeorchis, Cyrtopodium, Dactylostalix, Eulophia, Eulophidium, Eulophiella, Galeandra, Geodorum, Govenia, Graphorkis, Lissochilus, Pteroglossaspis, Tipularia, Warrea, Yoania.

DENDROBIINAE Bentham (Bulbophyllinae Schltr.)

We follow Bentham in associating *Dendrobium* and *Bulbophyllum* in a separate subtribe. We do not doubt that *Dendrobium* is related to *Eria*, but the relationship to *Bulbophyllum* is much closer, and the naked pollinia of this group are quite distinctive. *Dendrobium* and *Bulbophyllum* are primarily distinguished by the position of the inflorescence, and even this is subject to exceptions, as in *D. laterale* L. Wms. The embryological data also support a close relationship between these genera (Swamy, 1949). These are probably the largest genera of the orchids, as now treated. Holttum (1953) notes that the sections of *Dendrobium* are biologically far more distinct than many orchid genera in other subtribes. It may be that the naked pollinia severely limit the possibilities of morphological variation in flower structure. Generic limits in the Liparidinae (with naked pollinia) are similarly difficult. If this hypothesis is correct, the Genyorchidinae, which are surely derived from *Bulbophyllum*-like ancestors, may have escaped these limitations by the development of stipes, and show correspondingly greater variation in flower structure.

Bulbophyllum, Dendrobium, Epigeneium, Pedilochilus, Pseuderia, Saccoglossum.

EPIDENDRINAE (Eriinae Bentham, Laeliinae Bentham, Stenoglossinae Bentham, Podochilinae Bentham & Hooker, Cattleyinae Pfitzer, Ponerinae Pfitzer, Glomerinae Schltr., Polystachyinae Schltr., Epidanthinae L. Wms.)

We are relatively familiar with the genera of this group, especially the American ones, and we have found it necessary to unite several previously recognized

subtribes under this one. It is quite possible that some of the alliances which are discussed below will eventually prove to deserve subtribal status, but we are unable to find any feature or combination of features which will convincingly separate them. The key features which have been used are largely imaginary. The name Epidendrinae is required for the subtribe of the Epidendreae which includes the type genus. Hawkes and Heller (1959) list the "subtribe Stolziinae," but we have not been able to locate any valid publication of such a name. Schlechter (1926) and Summerhayes (1953) agree that *Stolzia* is closely related to *Polystachya.*

Key to Alliances

1. Pollinia laterally flattened or subglobose, 2–8 2
1. Pollinia clavate, 4–8 4
2(1). Plants African (except for some species of *Polystachya*—pseudobulbous plants with terminal raceme, a distinct column foot, 2–4 pollinia, a distinct viscidium, and the callus of the lip usually with mealy hairs) .... *Polystachya* alliance
2. Plants not African 3
3(2). Plants American; pollinia 2–8; inflorescence usually terminal .... *Epidendrum* alliance
3. Plants Asiatic; pollinia 8; inflorescence usually upper axillary .... *Eria* alliance
4(1). Rostellum elongate, beak-like; anther dorsal 7
4. Rostellum short, not markedly projecting nor beak-like; anther more or less terminal 5
5(4). Plants American, with slender, unifoliate stems, fleshy leaves and a dense spike of small rose-purple flowers .... *Arpophyllum* alliance
5. Plants of Old World 6
6(5). Viscidium well developed; flowers usually in dense subcapitate clusters .... *Glomera* alliance
6. Viscidium usually absent; flowers not in dense subcapitate clusters .... *Eria* alliance
7(4). Asiatic plants with elongate stems and distichous leaves .... *Podochilus* alliance
7. American plants with short, unifoliate stems (*Meiracyllium*) .... *Arpophyllum* alliance

a. Arpophyllum alliance

These two genera stand apart from the *Epidendrum* alliance in the possession of clavate rather than laterally flattened pollinia. The form of the pollinia and viscidium ally them to the *Glomera* and *Podochilus* alliances, and, especially, to the Pleurothallidinae, with which they agree in habit. They probably represent the ancestral stock of this distinctive American subtribe.

Arpophyllum, Meiracyllium.

b. Epidendrum alliance

The classic distinction between the Laeliinae and the Ponerinae; the presence or absence of a column foot, is clearly an unnatural one, and largely a matter of degree. The column foot is slight in several of the genera, and, in fact, is present in some species of *Laelia* (in the section *Schomburgkia*). Several genera have been repeatedly shifted between the two groups, as for example *Domingoa, Nageliella* and *Hexisea. Domingoa,* though closely related to *Nageliella* and *Scaphyglottis,* has been crossed with *Encyclia. Nageliella* is clearly allied to some of the elements of the *Scaphyglottis* complex; and *Homalopetalum, Hexisea* and *Nidema,* similarly, show greater affinity to *Scaphyglottis* than to the other plants customarily included in the Laeliinae.

Williams has separated *Epidanthus* as a subtribe, on the basis of a distinct

viscidium. Such a viscidium, however, is found in most species of *Epidendrum*. *Epidanthus* is distinctive in the possession of only two pollinia, but in all other features it resembles true *Epidendrum*.

This alliance appears to be the most distinctive of those included here, and it is possible that it is not as closely related to *Eria* as the structure of *Ponera*, especially, suggests. It may be that the resemblances between *Ponera* and *Eria* are parallelisms, and not indicative of close relationship. We are reluctant, though, to recognize subtribes on the basis of distribution alone.

Alamania, Barkeria, Brassavola, Broughtonia, Cattleya, Caularthron, Constantia, Dimerandra, Diothonaea, Domingoa, Encyclia, Epidanthus, Epidendrum, Hexisea, Homalopetalum, Isabelia, Isochilus, Jacquiniella, Laelia, Leptotes, Loefgrenianthus. Nageliella Neocogniauxia, Nidema, Octadesmia, Orleanesia, Platyglottis, Ponera, Scaphyglottis, Sophronitella, Sophronitis, Tetramicra.

c. Eria alliance

This group is not clearly separable from either the *Epidendrum* alliance or the *Polystachya* alliance. The three may be thought of as the American, Asiatic and African segments of a single complex, though a few species of *Polystachya* are widespread.

Cryptochilus, Eria, Porpax.

d. Glomera alliance

These genera are very closely allied to *Eria*, though the viscidium is better developed. The two groups may not merit separation, even as alliances.

Aglossorhyncha, Agrostophyllum, Ceratostylis, Chitonochilus, Cyphochilus, Earina, Epiblastus, Giulianettia, Glomera, Glossorhyncha, Ischnocentrum, Mediocalcar, Poaephyllum, Sarcostoma, Sepalosiphon.

e. Podochilus alliance

This group is closely allied to the *Glomera* alliance, and differentiated primarily by the more elongate rostellum.

Appendicula, Chilopogon, Podochilus.

f. Polystachya alliance

These genera show little affinity to the other genera grouped in the Polystachyinae by Schlechter. *Neobenthamia* has four laterally flattened pollinia and an indistinct viscidium (many species in the *Epidendrum* alliance have the viscidium better developed), while *Stolzia* has eight pollinia and no viscidium. *Polystachya* has a distinct viscidium and the pollinia are united into two in some species, while others bear four laterally flattened pollinia, as in the majority of the Epidendrinae. Some species of *Polystachya* have a small but distinct stipe, while this is not evident in other species which we have examined.

Neobenthamia, Polystachya, Stolzia.

Gastrodiinae Pfitzer

The Gastrodiinae are all saprophytic, and the flowers are tubular in most species.

They are apparently allied to the Vanillinae and Pogoniinae. *Stigmatodactylus* is clearly out of place in the Chloraeinae (Acianthinae), and appears to be closely allied to *Didymoplexis* section *Leucolaena* (*Didymoplexiella*).

Auxopus, Didymoplexis, Gastrodia, Stigmatodactylus?, Uleiorchis.

Genyorchidinae Schltr.

This group is allied to the Dendrobiinae, and especially to *Bulbophyllum*, but apparently differs in the possession of a distinct stipe or stipes.

Drymoda, Genyorchis, Ione, Monomeria.

Liparidinae Bentham (Microstylidinae Bentham, Malaxidinae Bentham & Hooker, Vargasiellinae C. Schweinf. [not validly published])

This subtribe, like the Dendrobiinae, is distinctive in the possession of completely naked pollinia. A viscidium is sometimes developed, but caudicles are lacking. The systematic position of the Liparidinae is not well understood. Mansfeld suggests a relationship to the Cyrtopodiinae (Calypsoinae), as well as to the Neottiinae (tribe Neottieae), but neither relationship is well documented. Clearly, this group deserves further study.

The subtribe Vargasiellinae was proposed without description, and is thus not validly published. The only clear feature we can find which might be taken to distinguish *Vargasiella* from the Liparidinae is the distinct claw of the lip. The habit is distinctive among the American genera, but is less so when Old World genera are considered. This genus should also be compared with *Pseuderia* (Dendrobiinae).

Didiciea?, Ephippianthus?, Hippeophyllum, Imerinaea, Liparis, Malaxis, Oberonia, Orestia, Risleya, Vargasiella.

Maxillariinae Bentham (Huntleyinae Schltr., Lycastinae Schltr., Zygopetalinae Schltr.)

We are unable to separate the Huntleyinae and Zygopetalinae even as alliances (see below). The close relationship between the *Lycaste* and *Zygopetalum* alliances is confirmed by artificial hybrids such as *Zygocaste*. The *Maxillaria* alliance is superficially separated from the *Lycaste* alliance by the conduplicate leaves, but floral structure indicates a close relationship. The structure of the pollinia is similar in *Xylobium*, *Bifrenaria* and *Maxillaria*. Of interest is *Bifrenaria minuta* Garay, which has slightly plicate leaves, but is otherwise a *Maxillaria*. We know of a hybrid between *Lycaste virginalis* and *Maxillaria variabilis*, though none of the plants has yet flowered. The difficulty of raising *Lycaste* seedlings to maturity is probably one reason that no such hybrids are yet registered.

Key to Alliances

1. Callus usually wide, with conspicuous longitudinal ridges.......................*Zygopetalum* alliance
2. Callus usually narrow, smooth...2
2(1). Leaves plicate...*Lycaste* alliance
2. Leaves conduplicate...*Maxillaria* alliance

a. Lycaste alliance

We have placed *Teuscheria* here, though its author assigned it to the *Bletiinae.* The shape of the anther and the four superposed pollinia with a distinct viscidium (large in *T. pickiana,* quite small in *T. venezuelana*) support this classification. The genus is described as lacking a viscidium, but we do not understand "Pollinia . . . inappendiculata, visco parco cohaerentia, sine glandula." The viscidium (and the resupinate flower) is clearly shown in Mrs. Allen's illustration of *T. pickiana* (Ceiba 4:272. 1955). *Neomoorea* and *Eriopsis* are assigned to the Zygopetalinae by Mansfeld (1937), but appear to fit as well or better in the *Lycaste* alliance.

Anguloa, Bifrenaria, Eriopsis?, Lycaste, Neomoorea?, Rudolfiella, Teuscheria, Xylobium.

b. Maxillaria alliance

Hoehne has separated some of the monopodial Maxillarias as a distinct genus, *Marsupiaria,* but it is doubtful that this is a natural group. *Maxillaria valenzuelana,* for example, is extremely closely related to *M. crassifolia* (a sympodial species) in all floral features, and seedlings of *M. crassifolia* have the habit of *M. valenzuelana.*

Chrysocycnis, Cyrtidium, Maxillaria, Mormolyca, Pityphyllum, Scuticaria, Sepalosaccus, Trigonidium.

c. Zygopetalum alliance

The Huntleyinae are traditionally separated from the Zygopetalinae by the conduplicate leaves, but this distinction is not usable. The leaves are subplicate in most species. We have observed cases in both *Zygopetalum mackayi* and *Cochleanthes flabelliformis* in which young growths with conduplicate vernation were seen in the same plant with growths of distinctly convolute vernation. The genera assigned to the Zygopetalinae usually have pseudobulbs, while those assigned to the Huntleyinae usually have the pseudobulbs inconspicuous or none. Some genera of this alliance, such as *Otostylis,* strongly resemble the Cyrtopodiinae, and suggest the origin of this subtribe from *Eulophia*-like ancestors.

Aganisia, Batemannia, Bollea, Cheiradenia, Chondrorhyncha, Cochleanthes, Colax, Galeottia, Huntleya, Koellensteinia, Menadenium, Neogardneria, Otostylis, Paradisianthus, Pescatoria, Promenaea, Stenia, Wareella, Zygopetalum.

Oncidiinae Bentham (Notyliinae Bentham, Adinae Pfitzer, Aspasiinae Pfitzer, Ionopsidinae Pfitzer, Odontoglossinae Pfitzer, Trichopiliinae Pfitzer, Brachtiinae Schltr., Campanemiinae Schltr., Cochliodinae Schltr., Comparettiinae Schltr., Dichaeinae Schltr., Lockhartiinae Schltr., Macradeniinae [Mansf.] Schltr., Ornithocephalinae Schltr., Papperitziinae Schltr., Pterostemminae Schltr., Saundersiinae Schltr., Telipogoninae Schltr., Trichocentrinae Schltr.)

It is in this group that we have committed the most wholesale reduction of subtribes. These changes, however, are required not only by the rapidly accumulating evidence of intergeneric fertility (see Moir, 1959), but by the patterns of morphological variation as well. Some of the "genera" placed in separate subtribes by Schlechter can not be distinguished by any feature known to us.

Key to Alliances

1. Pollinia 2 .... *Oncidium* alliance
1. Pollinia 4 2
2(1). Column with elongate, beak-like rostellum; lip not anchor-shaped... *Ornithocephalus* alliance
2. Column with a short rostellum, not beak-like; lip usually anchor-shaped......... *Dichaea* alliance

a. Dichaea alliance

This genus is distinctive in habit and aspect, but closely related to the *Ornithocephalus* alliance. The pilose column with a "ligule" on the ventral surface is also found in *Telipogon* and allied genera.

Dichaea.

b. Oncidium alliance

It might seem, from a survey of Schlechter's classification, that there would be a valid break within this group into two major alliances, those with spurs and those without. The presence or absence of a spur, however, is not consistent within the genera, and these groups are nearly all interfertile. We have successfully crossed *Comparettia* with *Oncidium, Trichocentrum, Trichopilia* and *Ionopsis. Rodriguezia,* similarly, is interfertile with a wide range of genera. *Trichopilia* is superficially distinct, in that the base of the lip enfolds the column, but this same feature is found in some species of *Miltonia. Notylia* is unusual in the dorsal position of the anther, but this, too, is inconsistent. *Lockhartia* is distinctive in habit, but has no other consistent feature to distinguish it from the other genera of this group. *Pterostemma* is poorly known, but its monopodial habit can not be taken to exclude it from this subtribe.

Ada, Amparoa, Aspasia, Brachtia, Brassia, Capanemia, Caucaea, Chaenanthe, Cochlioda, Cohniella, Comparettia, Diadenium, Erycina, Gomesa, Hybochilus, Ionopsis, Leochilus, Lockhartia, Macradenia, Mesospinidium, Miltonia, Neodryas, Neokoehleria, Notylia, Odontoglossum, Oncidium, Papperitzia, Petalocentrum, Polyotidium, Plectrophora, Pterostemma, Quekettia, Rodriguezia, Rodrigueziopsis, Roezliella, Rusbyella, Sanderella, Saundersia, Scelochilus, Sigmatostalix, Solenidium, Systeloglossum, Sutrina, Theodorea, Trichocentrum, Trichopilia, Trizeuxis, Warmingia.

c. Ornithocephalus alliance

These genera are distinguished from the *Oncidium* alliance only by the number of pollinia, but they do form a somewhat distinctive group. There is no way, however, to separate the Telipogoninae and the Ornithocephalinae. Many of the Telipogoninae are distinctive in that they apparently mimic insects (as in many species of *Ophrys*), and in the pilose column and hooked viscidium, but these latter features are matched by *Cordanthera* and some species of *Dipteranthus*.

Centroglossa, Chytroglossa, Cordanthera, Cryptarrhena, Dipteranthus, Dipterostele, Hintonella, Hofmeisterella, Oakes-amesia, Ornithocephalus, Phymatidium, Platyrhiza, Sodiroella, Sphyrastylis, Stellilabium, Telipogon, Thysanoglossa, Trichoceros, Zygostates.

Pachyphyllinae Pfitzer

Though distinguished by the differently shaped column and consistently monopodial habit, these genera seem closely allied to the Maxillariinae. *Pachyphyllum*

and *Chrysocycnis*, especially, appear to be closely allied, and resemble each other in habit, inflorescence and 3-winged ovary.

Centropetalum, Pachyphyllum.

PLEUROTHALLIDINAE Bentham

These genera form a distinctive American group most closely allied to the Epidendrinae, especially to the *Arpophyllum* alliance.

Acostaea, Barbosella, Brachionidium, Cryptophoranthus, Lepanthes, Lepanthopsis, Masdevallia, Octomeria, Physosiphon, Platystele, Pleurothallis, Pleurothallopsis, Porroglossum, Restrepia, Scaphosepalum, Stelis, Yolanda.

POGONIINAE Pfitzer (Nerviliinae Schltr.)

We follow Mansfeld in separating the Vanillinae and the Pogoniinae, and including *Nervilia* in the Pogoniinae. The flower structure of *Nervilia* is quite comparable to that of the other Pogoniinae, and most species were first described under *Pogonia*. The habit is somewhat distinctive. These genera are similar in floral structure to both the Vanillinae and the Sobraliinae. The pollen is quite mealy, but they lack the distinctive seed structure of the Vanillinae.

Cleistes, Isotria, Lecanorchis, Monophyllorchis, Nervilia, Pogonia, Pogoniopsis, Psilochilus, Triphora.

RIDLEYELLINAE Schltr.

The habit of this genus is suggestive of *Bulbophyllum*, and the pollinia are said to be naked, though the floral structure is otherwise more reminiscent of the Thelasiinae.

Ridleyella.

SARCANTHINAE Bentham (Aeridinae Pfitzer)

This is the great group of primarily Old World monopodial orchids. In floral specialization and complexity they parallel the American Oncidiinae and are not easily "keyed" from the monopodial Oncidiinae, though there is probably no close relationship. Note that this group must be known as the Vandinae if the tribe Vandeae is maintained. Hawkes and Heller (1959) list the "subtribe Campylocentrinae." This name is listed by Hoehne in Flora Brasilica (12^1:23, 39), but we cannot find that it has ever been formally proposed, nor can we find any reason that it should be.

Abdominea, Acampe, Adenoncos, Aerangis, Aeranthes, Aerides, Ambrella, Ancistrorrhynchus, Angraecopsis, Angraecum, Ankylocheilos, Arachnis, Armodorum, Ascocentrum, Ascochilopsis, Ascoglossum, Barombia, Bathiea, Beclardia, Bogoria, Bolusiella, Bonniera, Calymmanthera, Calyptrochilum, Camarotis, Campylocentrum, Ceratochilus, Chamaeangis, Chamaeanthus, Chauliodon, Cheirorchis, Chiloschista, Chroniochilus, Cottonia, Crossangis, Cryptopus, Cyrtorchis, Dendrophylax, Diaphananthe, Dinklageella, Diplocentrum, Diploprora, Dryadorchis, Eggelingia, Encheiridion, Esmeralda, Eurychone, Finetia, Fitzgeraldiella, Gastrochilus, Holcoglossum, Hymenorchis, Jumellea, Lemurella, Lemurorchis, Listrostachys, Luisia, Macropodanthus, Malleola, Microcoelia, Microsaccus, Microtatorchis, Mystacidium, Nephrangis, Neobathiea, Oeonia, Oeoniella, Omoea, Ornithochilus. Pelatantheria, Pennilabium, Perrierella, Phalaenopsis, Phormangis, Phragmorchis, Plectrelminthes, Podangis, Polyrhiza, Pomatocalpa, Porphyrodesme, Rangaeris, Renanthera,

Renantherella, Rhipidoglossum, Rhynchostylis, Robiquetia, Saccolabiopsis, Saccolabium, Sarcanthus, Sarcochilus, Sarcorrhynchus, Schoenorchis, Solenangis, Sphyrarhynchus, Staurochilus, Stauropsis, Taeniophyllum, Taeniorrhiza, Thrixspermum, Triceratorhynchus, Trichoglottis, Tridactyle, Uncifera, Vanda, Vandopsis, Ypsilopus.

SOBRALIINAE Schltr. (Palmorchidinae Schweinf. & Correll [not validly published])

These genera were included in the Neottieae by Schlechter, but the pollinia are more or less waxy in many species, and the flower structure agrees well with that of the Epidendrinae and Thuniinae. Mansfeld actually assigns the Thuniinae to this subtribe, though we believe this action to be questionable, at least without more detailed knowledge of the Thuniinae. Schweinfurth has evidently abandoned the use of the subtribe Palmorchidinae, which was proposed without description. In no case did Schweinfurth and Correll assign *Corymborchis* to the Palmorchidinae, an action which would scarcely have been defensible (see, however, Hawkes & Heller, 1959).

Diceratostele, Elleanthus, Palmorchis, Sertifera, Sobralia, Xerorchis.

STANHOPEINAE Bentham (Gongorinae Schltr.)

This group is not clearly distinguished from the Maxillariinae (*Lycaste* alliance), though the more bizarre genera (*Stanhopea, Coryanthes,* etc.) are easily distinguished. More study of this group is needed.

Acineta, Chaubardia?, Cirrhaea, Coeliopsis, Coryanthes, Endresiella, Gongora, Gorgoglossum, Houlletia, Kegeliella, Lacaena, Lueddemannia, Lycomormium, Paphinia, Peristeria, Polycycnis, Schlimia, Sievekingia, Stanhopea, Trevoria.

THECOSTELINAE Schltr.

The flower structure of *Thecostele* is quite bizarre, but adequate knowledge of all species may indicate that it should be included in the Genyorchidinae.

Thecostele.

THELASIINAE Schltr.

The Thelasiinae are small Asiatic plants which are distinctive in habit and inflorescence. The pollinia have been described as having a stipe, but this appears to be an unusually long caudicle (Mansfeld, 1937b).

Chitonanthera, Octarrhena, Oxyanthera, Phreatia, Rhynchophreatia, Thelasis.

THUNIINAE Schltr. (Claderiinae Mansf. [not validly published])

Tall Asiatic plants with slender stems and rather showy flowers, in habit these plants (especially *Arundina*) closely resemble the Epidendrinae. In the structure of the column, however, they more closely resemble *Coelogyne* and *Phajus*. *Bromheadia* was placed in the Polystachyinae by Schlechter, but is surely out of place there (see Ridley, 1891). It resembles *Dilochia* in habit and appears to resemble *Claderia* in flower structure. Unfortunately, we have seen too little of all these genera. The group is unusually diverse in the structure of the pollinia, and it is possible that further study will show it to be unnatural. The subtribe Claderiinae was proposed without description.

Arundina, Bromheadia?, Claderia, Dilochia, Thunia.

VANILLINAE Bentham

These genera are, in several features, among the most primitive in the subfamily. They are included in the Pogoniinae by Schlechter, but the habit and distinctive seed structure would seem to justify their separation, as indicated by Mansfeld. They also show some affinity to the Sobraliinae, but there is little evidence of close alliance with the Neottieae.

Duckeella, Epistephium, Eriaxis, Galeola, Vanilla.

SUBTRIBES OF UNCERTAIN AFFINITY

GROBYINAE Schltr.

This genus has been placed near the Cymbidiinae in most systems, but this seems to be questionable. We have not seen adequate material, but a comparison with the Maxillariinae may be in order.

Grobya.

PACHYPLECTRINAE Schltr.

This genus is known only from New Caledonia. It apparently belongs to the Neottieae, but Schlechter's description is not adequate for more exact placement. It may be allied to the Diuridinae and Cryptostylidinae.

Pachyplectron.

PHYLOGENY

There are two extremes in the variation patterns shown by living plant groups, depending apparently on rates of evolution and amount of extinction. At one end of the spectrum stand such families as the Magnoliaceae, Annonaceae and Nymphaeaceae. These families have the appearance of being "old" groups, in which evolution is proceeding at a leisurely pace and extinction has greatly affected the pattern of variation. Such groups as the cacti and the Euphorbiaceae-Euphorbieae represent the other extreme. They show little evidence of great age, show signs of relatively rapid diversification in geologically recent time, and give much less evidence of extinction. Our classification of genera and higher groups is in large measure based on extinction, and so we have very different problems with these two types. The delimitation of genera and tribes within the Magnoliaceae or the Nymphaeaceae is not difficult. We are often at a loss, though, to understand their relationships or phylogeny.

As should now be clear, the orchids are near the other end of our spectrum in these features. Genera are often difficult to define, and higher categories within the family seem even worse. These hazy boundaries between tribes and subtribes, however, may give clues to the patterns of phylogeny within the family. We do not mean to imply that living groups can often be derived from other living groups, but one can find excellent evolutionary series for nearly every morphological feature within the orchids. In recent years there has been a healthy skepticism concerning phylogenetic schemes (see especially Sporne, 1959). Even

when one can find a good morphological series in some feature, it is often difficult to decide in which direction or directions evolution has occurred. This problem is not so serious in a highly derived group such as the Orchidaceae. In comparing *Cephalanthera* and *Oncidium* there can be little doubt as to which is derived and which is primitive. In nearly every feature in which these two differ, it is *Cephalanthera* which is the ordinary monocot, easily comparable with other monocot families, while *Oncidium* can scarcely be understood without comparing it with the less specialized members of the family. One would scarcely expect to derive whorls of separate stamens and pistils from the column of the advanced Epidendreae, but the evolution of the column from primitively free parts is easily understood and partially documented among the living orchids. As an actively evolving group in which the patterns of evolution are unusually clear, the orchids are especially appropriate for evolutionary study and may throw a good deal of light on parallelism, polyphylesis and other problems which plague the biologist dealing with apparently more ancient groups.

When one studies the relationships of the subtribes, a pattern takes shape, and one may form a rather clear idea of the over-all evolutionary patterns for the family. The pattern of relationships for the Epidendreae (fig. 1) scarcely provides a classic dendrogram, but there are clear indications of primitive groups and some indications of the patterns of evolution which may have occurred. These may best be considered by discussing evolution in particular features of the plant.

Habit

As Holttum (1955) has shown, the predominant growth form in a wide range of monocots is the sympodium, and we may reasonably consider this to be the primitive condition in the orchids. The majority of primitive orchids have a rather ordinary monocot habit, as for example *Cephalanthera,* with a short rhizome and erect, non-thickened annual stems with scattered, spiral leaves and a terminal inflorescence. The origin of the majority of other sympodial growth forms by phyletic shortening and/or thickening of the stems is readily envisioned. Of special interest is the monopodial habit, in which the stem has unlimited apical growth and roots are not restricted to the basal portion. In some systems this has been considered to be the distinguishing mark of the Sarcanthinae. We find, however, that the monopodial habit occurs in the Vanillinae, Cymbidiinae, Maxillariinae, Pachyphyllinae, Cryptocentrinae, Thelasiinae and Oncidiinae, and possibly in other groups as well. In some of these groups we have a good graded series from sympodial plants to related monopodial types. Not only does the monopodial habit appear to have evolved independently in many groups, but its evolution seems to have followed somewhat different patterns in different cases. In the Vanillinae and the Sarcanthinae it has apparently been the simple retention of apical growth in the members of a sympodium (with lateral inflorescence). In some of the Maxillariinae and allied groups it appears to be the suppression of pseudobulbs on a leafy rhizome. In other cases, such as *Maxillaria valenzuelana,* and some Oncidiinae (*Oncidium pusillum* complex, *Rodriguezia* spp.), the monopodial habit

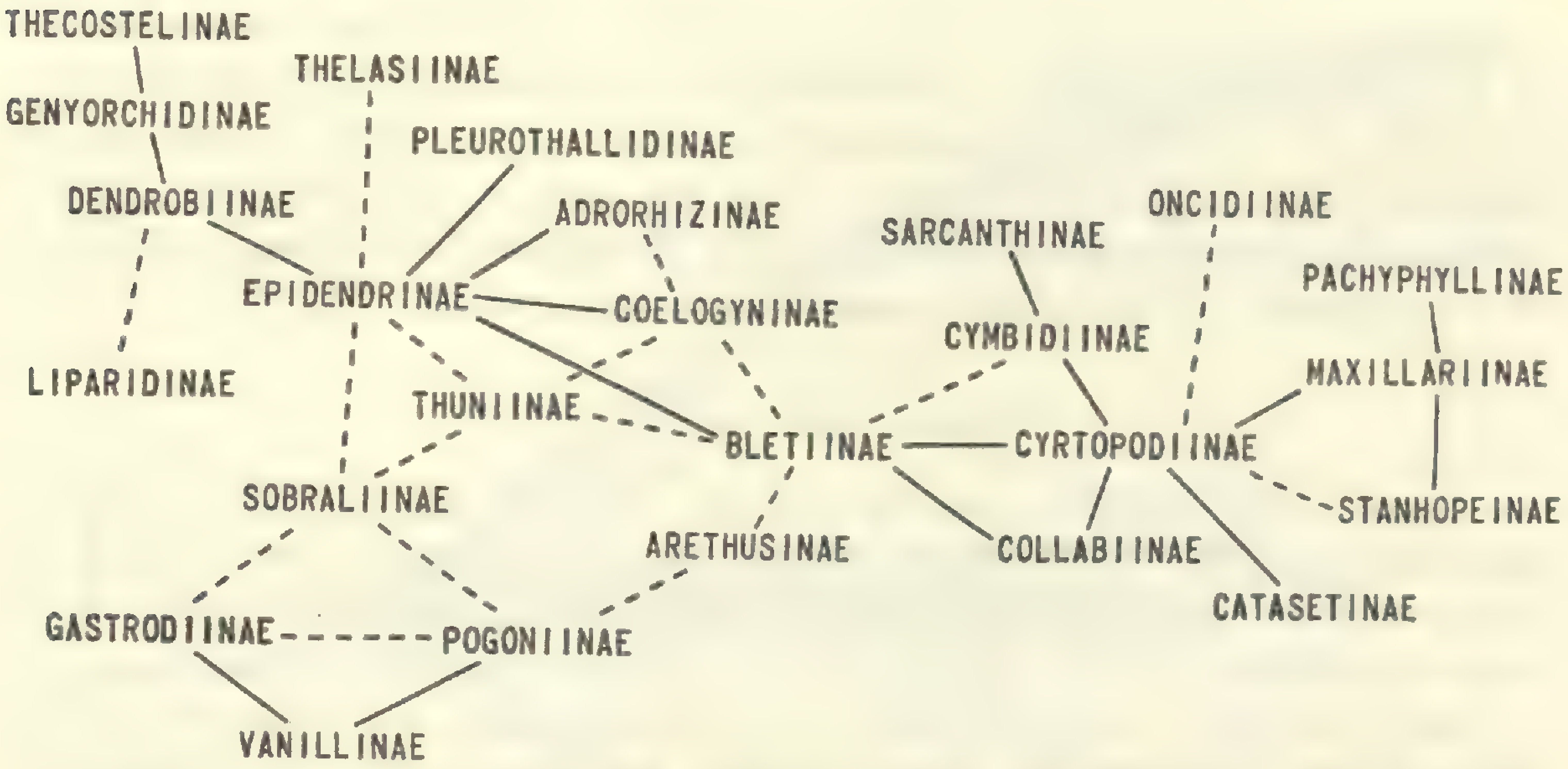

Figure 1. A diagram of suggested relationships within the tribe Epidendreae. Solid lines represent close relationships, while dashed lines represent relationships which are more distant or less clear.

seems to have evolved by the retention of a permanent juvenile form. In hybrid swarms involving *Rodriguezia refracta* (sympodial) and a related monopodial species one may find a complete series ranging from those plants which are monopodial only in the seedling stage to those which are monopodial for the life of the plant.

Kränzlin (1923) attempted to retain the monopodial habit as the distinguishing feature of the Sarcanthinae by classing *Dichaea, Lockhartia, Pterostemma* and the Pachyphyllinae as the heterogeneous "Pseudomonopodiales," pointing out that *Lockhartia* and some species of *Dichaea* are not strictly monopodial, in that the stems are erect, and of more or less limited growth, with roots and branches arising only at the base. While this is true, a very strict definition of the monopodial habit would also disqualify some Sarcanthinae (ex. *Mystacidium distichum*), and still leaves some undoubted monopodia in *Oncidium, Maxillaria,* and species of *Dichaea.* Though of considerable morphological and evolutionary interest, the monopodial habit has limited value as a taxonomic criterion.

Saprophytism

Saprophytic orchids are found in all three tribes of the Orchidoideae, and in at least twelve different subtribes. The majority of orchids pass through a saprophytic seedling stage, which may last for months, especially in terrestrial species. Thus, the evolution of a completely saprophytic life cycle in many different groups of orchids is not surprising. The wholly saprophytic orchids pose special taxonomic problems. The adaptations for saprophytism drastically change the vegetative features of the plant, thus obscuring some of the characteristics normally used in determining relationships. It may be that even the reproductive features are affected by these adaptations. In *Corallorhiza,* for example, we find the polliniar

apparatus to be simpler than in the related *Oreorchis* and *Tipularia.* In the absence of these closely allied genera, its relationship to the Cyrtopodiinae would be much less clear. The saprophytes are difficult to cultivate and poorly represented by herbarium specimens, which further complicates their study. Autogamy is frequent, and an autogamous saprophyte is nearly the ultimate in taxonomic difficulty. A special key to the saprophytic genera of orchids is needed.

Pseudobulbs and Corms

A great many orchids, and especially the epiphytic groups, show variously thickened stems or "pseudobulbs." While these structures are quite diverse in form, they fall into a limited number of morphological types and seem to show some evolutionary trends. One of these seeming trends is from pseudobulbs (or corms) of several or many internodes to pseudobulbs of a single internode (as in *Bulbophyllum,* Maxillariinae and Oncidiinae). Reference to the chart of relationships (fig. 1) suggests that there may be two basic patterns for the origin of pseudobulbs. In the majority of the Bletiinae, Cyrtopodiinae and related groups (the right side of fig. 1), pseudobulbs seem to have been derived phyletically from more or less corm-like structures, as in *Bletia* and *Phajus.* These thickened stem-bases may be found in either terrestrial or epiphytic groups, while the pseudobulbs of a single internode are restricted to primarily epiphytic groups. The other main pattern for the derivation of pseudobulbs appears to be shown by the Epidendrinae and some related groups (left side of fig. 1). In these groups corm-like structures are not found, and the pseudobulbs appear to have evolved by a phyletic thickening of the entire aerial shoot (as in *Dendrobium, Barkeria,* etc.). The more derived members of these groups may also possess pseudobulbs of a single internode, which are morphologically indistinguishable from those of the Oncidiinae or Maxillariinae (ex. *Bulbophyllum,* some species of *Dendrobium*).

Leaves

The evolutionary trends in leaf type seem rather clear, and have already been outlined by Rolfe (1909–1912). The primitive type of orchid leaf is probably non-articulate, wide (more or less elliptic) and plicate, of convolute vernation. The trends toward an articulate leaf which is narrow (more or less ligulate) and conduplicate, have probably occurred independently in several phyletic lines, and appear to be strongly correlated with the epiphytic habit. It is interesting that the monopodial orchids all have strictly conduplicate leaves, with the partial exception of *Vanilla,* which has convolute vernation, but the fleshy leaves of *Vanilla* are by no means plicate, and the mature leaf usually appears conduplicate. This points out the imperfect correlation between conduplicate leaves and duplicate vernation. The correlation is generally good, however. We have used plicate and conduplicate in the present paper, as terms descriptive of the mature leaf and therefore more readily determined. There are, of course, transitional stages, such as the many-veined but conduplicate leaves of most Cymbidiinae, which appear superficially plicate.

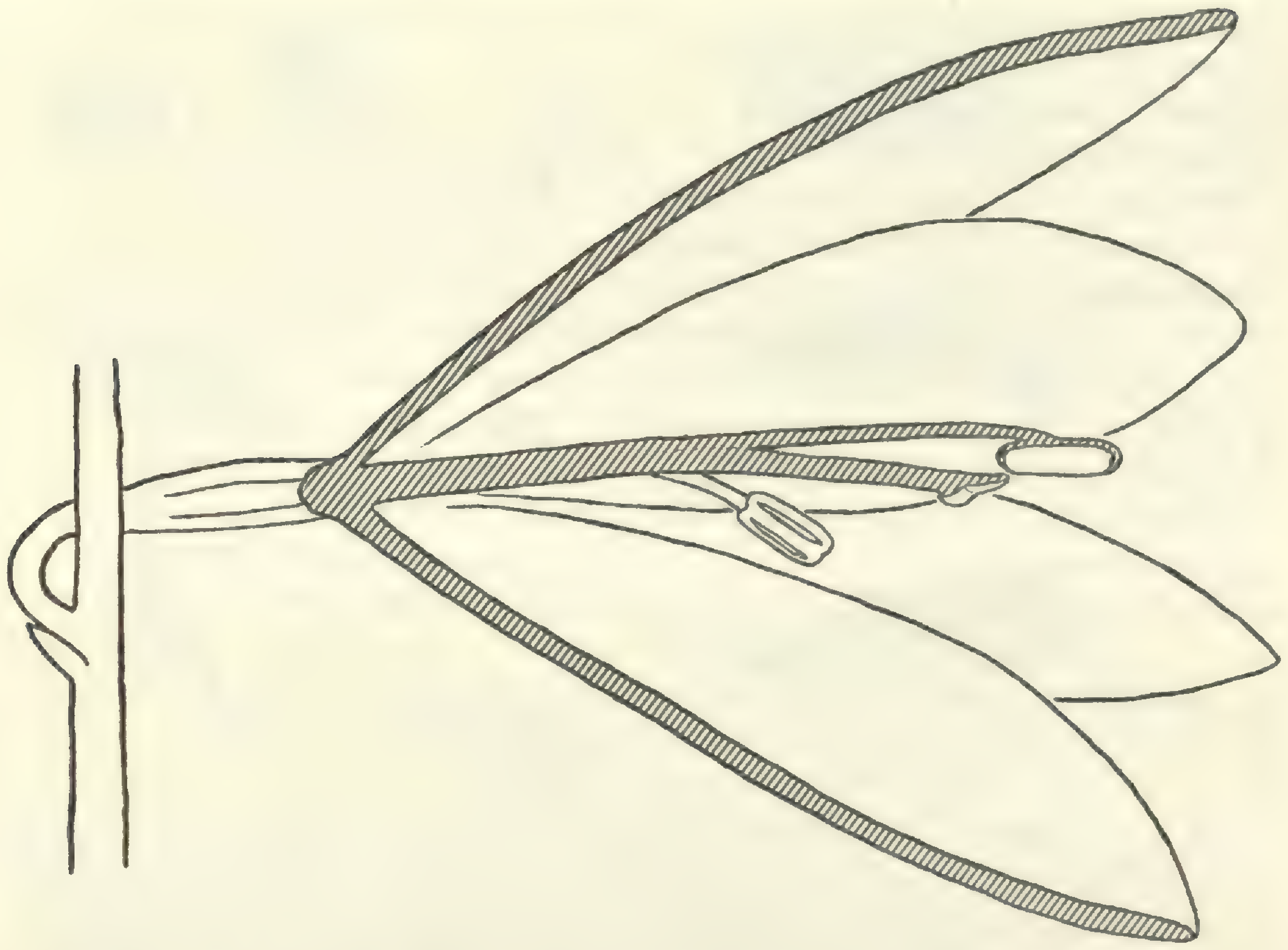

Figure 2. A longitudinal section of a hypothetical primitive orchid flower, highly schematic. In such a flower we would expect the perianth segments to be similar, and we would expect 3 anthers, one of which is borne above the stigma, the other two being lateral in position. Such a flower is closely matched in the living Apostasieae. A simple form of resupination is shown.

Flower

It is probable that the primitive orchid flower was a relatively unspecialized monocot flower with equal and similar perianth parts, similar to that now found in the Apostasieae. Such a hypothetical primitive orchid flower is sketched in fig. 2. The only unusual feature of the simpler orchid flowers is a certain degree of zygomorphy in the androecium. The three anthers which are found in the orchids are all on the abaxial side of the flower and are members of two different whorls. The adaxial stamens were evidently lost at an early stage in orchid evolution. In some groups of ancestral orchids, as in the living *Cephalanthera,* the viscid matter of the relatively unspecialized stigma may have served to glue the pollen masses of the median anther to the pollinating agent on its withdrawal from the flower. Such a relationship was surely the basis for the evolution of those tribes in which only the median anther is functional. A tremendous diversity exists in the form of the column and anther among living orchids. So great is this diversity in form and position that it is very difficult to use a precise terminology for the anther and its parts. The column itself has clear dorsal, ventral and lateral aspects (though morphologically confused by resupination, in which the adaxial side of the flower becomes ventral).

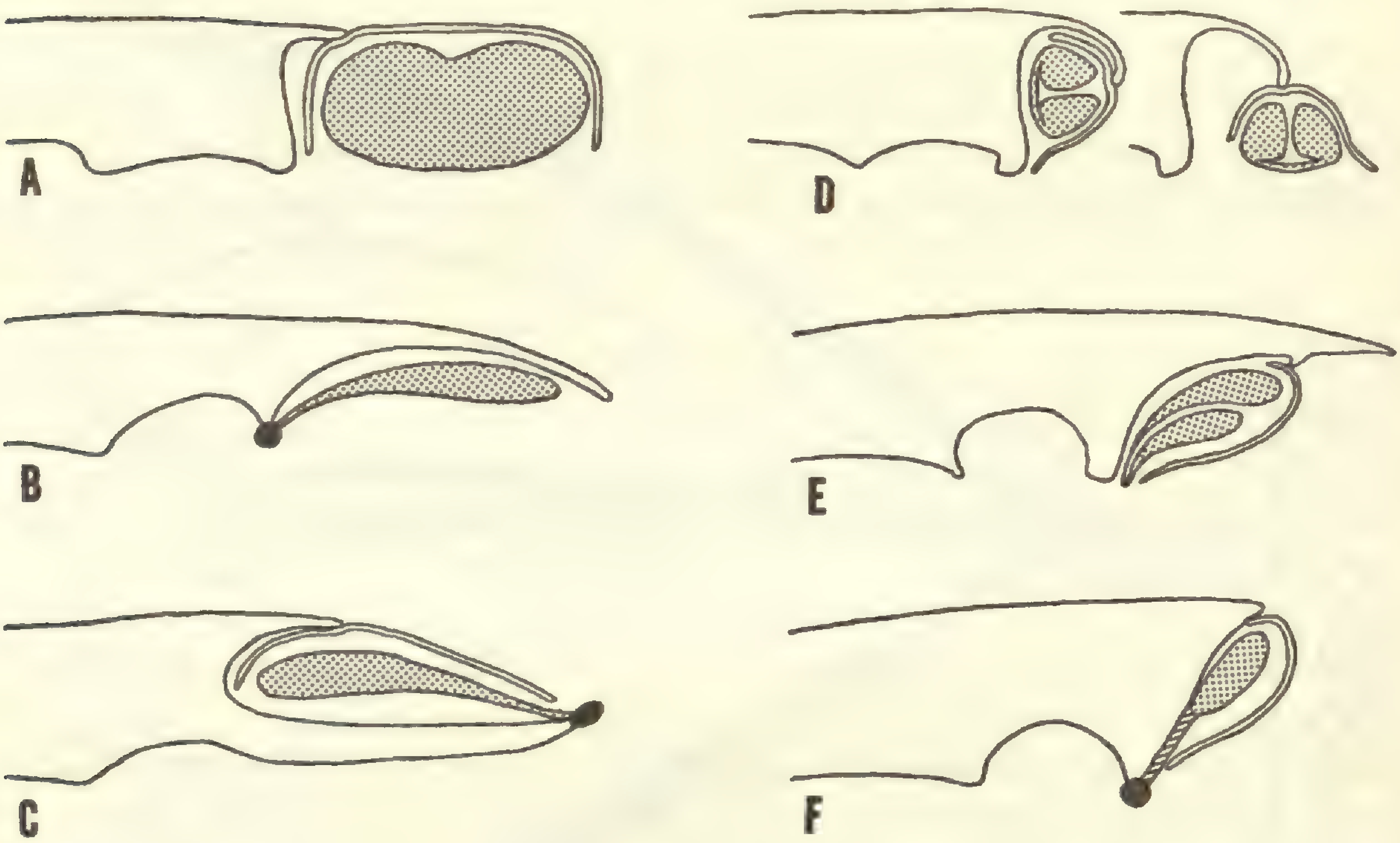

Figure 3. Diagrammatic longitudinal sections of orchid columns, showing the relationships of anther, pollen and stigma. Pollen is stippled; the viscidium, where present, is shown in black. A. A primitive orchid with the anther terminal and erect, the stigma is undifferentiated; *Cephalanthera.* B. A member of the Orchidinae, in which the anther is erect and broadly united to the column. The viscidium (or viscidia) is attached to the base of the pollinia. C. An orchid with dorsal anther; the rostellum is elongate and erect, with the viscidium attached to the apex of the pollinia; Spiranthinae, *Meiracyllium, Podochilus,* etc. D. An orchid with operculate, versatile anther; *Dendrobium, Cattleya, Vanilla,* etc. E. An orchid with ventral anther overtopped by the column, as in *Coelogyne.* F. An orchid with a more or less operculate anther and a distinct stipe (cross-hatched) attaching the pollinia to the viscidium. Typical of Sarcanthinae, Maxillariinae, Oncidiinae, etc.

Anther

In the subfamily Cypripedioideae three distinct stamens are usually present, though the median anther is represented by a staminode in *Apostasia* and the Cypripedieae. In the Orchidoideae it is only the median anther which is functional, the lateral anthers being completely absent or represented by staminodia. Three fertile anthers do occur as an occasional abnormality, and are the rule in a few autogamous forms. Vermeulen considers the auricles of *Cephalanthera, Epipactis* and the Orchideae not to be staminodia. Some other orchids, however, do bear distinct lateral staminodia. *Diuris* is probably the most noteworthy case, for here the staminodia are nearly as long as the style and are free nearly to their bases. Column wings or stelidia occur in a number of genera and are probably staminodia.

It is quite probable that the anther is primitively erect, and the anther is erect in the majority of living Neottieae. In the Spiranthinae, Diuridinae and related subtribes the anther is dorsal, and does not appreciably overtop the apex of the stigma. In these groups the pollinia are associated with the stigma by a terminal rostellum, and it may be that the dorsal anther is primitive for these groups. In this feature they are quite comparable to some of the Apostasieae. In the remaining

Neottieae the anther is normally terminal, usually reaching well beyond the stigma. Thus it is the basal or ventral portion of the pollinia which is usually associated with the rostellum in these subtribes. Such a condition was the probable starting point for the evolution of the Orchideae, for in this tribe the pollinia are attached to the viscidia by basal caudicles. In some members of this tribe the anther is erect and the anther cells fairly close together, the pollinia attaching to a single viscidium or two adjacent viscidia. This is, if not the primitive condition for the tribe, certainly the one most readily understood. In many members of the Orchidinae and Coryciinae the anther cells are widely separated and each pollinium is attached to a separate viscidium, the viscidia often being widely removed from the functional stigma. In the Disinae the anther is usually reclinate, being "bent" backwards from the column. In most species of *Satyrium* the anther actually has the base uppermost.

In the primitive Epidendreae the anther is normally incumbent and operculate on the apex of the column. In these subtribes the anther is actually more or less versatile, the (morphologically) ventral face of the anther resting against the apex of the column until the anther is rotated on the filament, as shown in fig. 3D. The anther is erect in the early floral ontogeny of these groups, and is erect in the mature flower of a few species. This probably represents an ontogenetic "reversion" in these plants, rather than a primitively erect condition, for they are all closely allied to species with fully incumbent anthers. In the more derived members of the Epidendreae the anther may take on almost any position: dorsal, terminal, ventral, or intermediate conditions which render accurate description and categorization difficult (see fig. 3).

Rostellum

The rostellum has been given as one of the family characteristics of the Orchidaceae. In its extreme development it is quite comparable to the situation in the Asclepiadaceae, in which part of the stigma has become associated with the pollen and takes part in the transfer of the pollen from anther to functional stigma. One finds, however, a complete series of gradations in the living orchids from forms with no structure which can be called a rostellum to the markedly complex structures in the advanced Oncidiinae and Sarcanthinae. The rostellum may perhaps be best defined as the structure separating the functional stigma from the anther, a portion of which serves to attach the pollinia to the pollinating agent. It is frequently stated to be the third (median) lobe of the stigma. As Vermeulen (1959) has shown, however, many orchids with a distinct rostellum have three stigma lobes, and the work of Wolf (1866) shows portions of the median lobe to be functionally stigmatic. Indeed, superficial observations suggest that the third stigma lobe may often be much the largest of the three. It would appear that only a portion of the third stigma lobe is involved in the rostellum, and it is not clear that other structures (such as style or filament) are not also involved. In the more highly evolved Orchidaceae the column behaves as a separate organ *sui generis*, the boundaries between the phyletically component parts being lost or

obscured. Vermeulen (1959) believes the rostellum of the Orchideae to be different in origin and nature from that of the Neottieae and Epidendreae, and suggests that it may be derived from the lateral stigma lobes. This does not seem to be supported by the developmental studies of Wolf (1866).

In its most primitive expression, in *Cephalanthera*, the entire stigma is functional as such, and the pollinia are normally attached to insects by a portion of the stigmatic fluid which the insects receive by brushing the stigma in retreating from the flower. In many groups of orchids a special part of the stigma is differentiated to supply the viscid material which attaches the pollinia to the pollinating agent, but the transfer is similar to that in *Cephalanthera.* In *Cattleya,* for example, the rostellum projects beyond the stigma, but the viscid matter and the pollinia do not come into actual contact without action of the pollinating agent. A slight further specialization is seen in *Sophronitis* and some species of *Calanthe,* where a portion of the rostellum is more or less differentiated as a viscid pad which is attached to the pollinia and is removed with them as a unit. This structure is variously known as viscidium, viscid disk or gland; we use the first term, as the structure is not a gland in the usual sense, nor is it usually a disk. In the more highly specialized groups, the viscidium is a sharply delimited structure attached to the pollinia by a strap of rostellar (or columnar) tissue which is not viscid. This connecting tissue is termed the stipe, and is cellular in structure, unlike the translator of the asclepiads. The high degree of diversity in rostellar structure, and the degrees of specialization within taxa suggest that, after the initial action of stigmatic fluid in transfer of pollen, all of the other specializations (viscidium and stipe) have arisen independently several or many times in separate phyletic lines. Early stages in the independent evolution of the viscidium are to be seen in several genera of the Epidendrinae, and the stipe appears to have evolved independently in the Prasophyllinae, Genyorchidinae, Spiranthinae, and perhaps elsewhere.

Pollinia

The major systems of orchid classification have focused attention on variation in the pollen and associated features. As in most other features, there is a high degree of diversity in the structure of the pollinia, but this diversity is accompanied by many gradations to a simple and unspecialized pollen. The simplest and surely most primitive condition is that in the Apostasieae. In this tribe we find unspecialized 4-locular anthers with powdery pollen. In the Cypripedieae the pollen grains are not united into larger units, but the pollen is somewhat viscid. In almost all members of the Neottieae and Orchideae the pollen grains are united into tetrads (free grains occur in *Cephalanthera*). Further, this granular pollen is usually loosely united into large masses by elastic threads of tapetal origin. These masses, or pollinia, may be two in number, each representing the contents of one half of the anther; more commonly the two halves are each more or less divided, so that each of four anther cells contains a pollen mass. The pollinia of the Orchideae are divided into many granular packets, interconnected by elastic threads. This is the condition termed sectile. In the Neottieae the pollinia are sectile only in the *Good-*

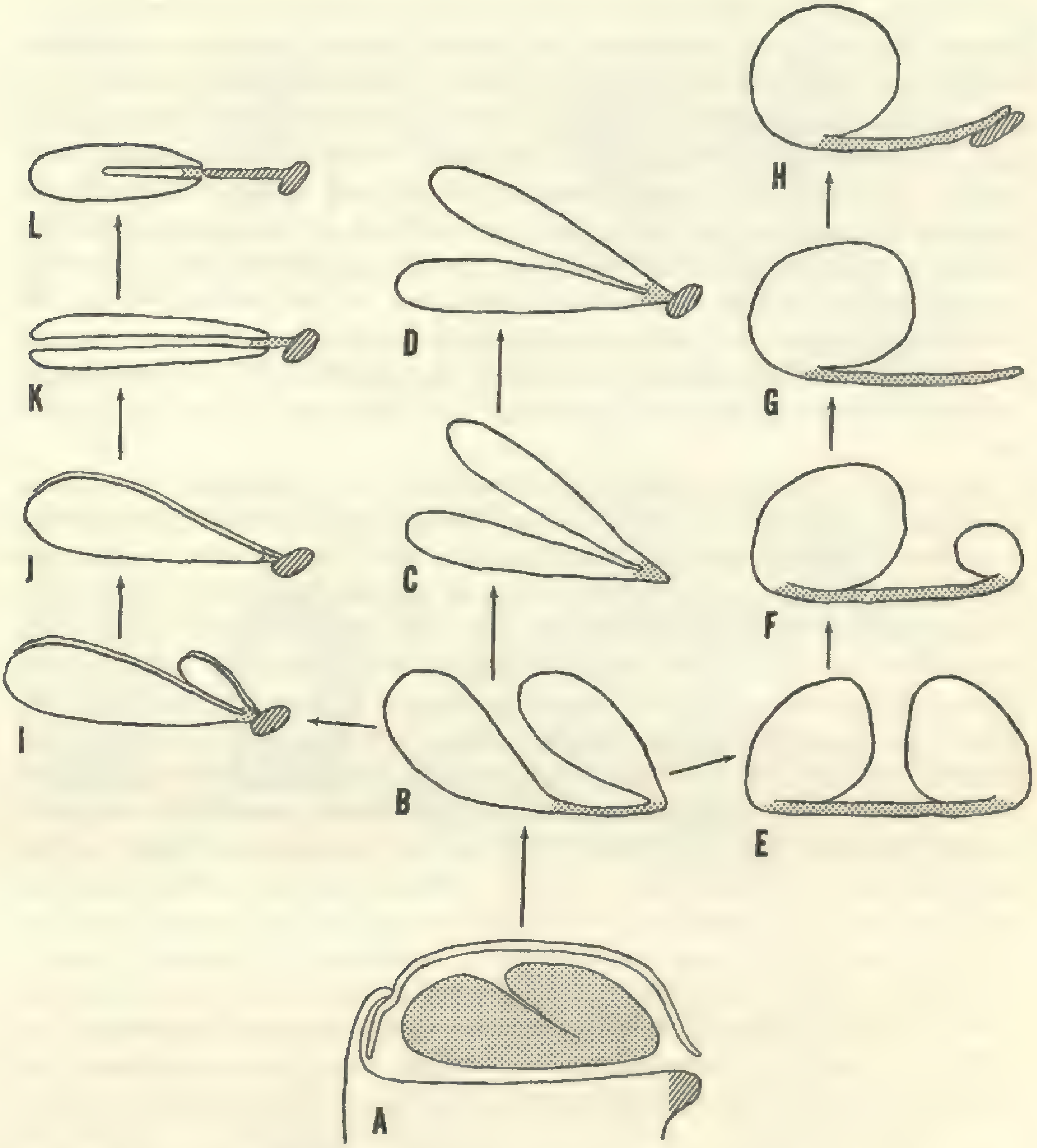

Figure 4. Diagram showing some of the major patterns of evolution in pollinia within the Epidendreae. Mealy pollen (only the caudicles in the higher forms) is stippled; the rostellum in A and the viscidium, where present, are cross-hatched. A. A relatively primitive orchid as in the Arethusinae or Sobraliinae, showing the orientation of the pollen within the anther and the position of the rostellum. In such an orchid there are 4 mealy pollinia, each more or less divided into 2 portions. Highly schematic. B–D. The evolution of clavate pollinia, as in Bletiinae and some sections of *Eria*. A viscidium may be formed (D). E–H. The major pattern of evolution in the *Epidendrum* and *Polystachya* alliances, in which 8 equal pollinia are reduced to 4 (rarely 2). A viscidium may be formed, but is usually attached to the pollinia by caudicles. I–L. The evolution of superposed pollinia, as in Cyrtopodiinae, Sarcanthinae, Maxillariinae and Oncidiinae. In the highly evolved forms the pollinia are frequently reduced to 2 in number and are attached to the viscidium by a stipe.

yera alliance. Sectile pollinia have, by some, been considered an intermediate step between mealy and waxy pollinia, but they represent rather a separate specialization. A single sectile pollinium may pollinate a number of separate flowers, as only a few of the packets are normally left in any one flower. In the Orchideae the basal portions of the pollinia form slender, sterile "caudicles" which attach the pollinia to the viscidia. The caudicles are largely composed of the elastic strands which unite the tetrads of the pollinium, but some tetrads may be found in the caudicles. Distinct caudicles are not formed in the Neottieae. In the Spiranthinae and some other subtribes the viscid disk is attached to the apices of the pollinia, but in the Australian Neottieae one finds a complete series from basal attachment through ventral to terminal attachment like that of the Spiranthinae. The distinction which has been drawn between "Acrotonae" and "Basitonae" is thus an artificial one.

In some of the more primitive groups of the tribe Epidendreae (Vanillinae, Pogoniinae, Arethusinae, some Bletiinae and Sobraliinae) granular or mealy pollinia occur, but the pollinia usually form hard, more or less "waxy" masses. In the more highly specialized groups the pollinia are quite compact and hard. In the Arethusinae and some Sobraliinae each of the four mealy pollinia is partly divided into halves. In most of the more primitive Epidendreae eight waxy pollinia occur. These are subclavate or laterally flattened and occur in two series, each basal pollinium being united to the terminal pollinium of the same anther cell by a band of granular pollinia which is strengthened by elastic strands, as in the caudicles of the Orchideae. These granular bands or caudicles may be united with each other so that the pollinia form two units of four each or a single unit of eight pollinia. In these groups it is the caudicle which is normally attached to the pollinating agent and provides a weak zone which can be stretched and broken when the pollinia contact the stigma of another flower. Reference is frequently made to "a caudicle having a viscid apex" or to "viscid disk arising from the apex of the pollinia." Such statements seem to represent translations from Schlechter's key (1926). As nearly as we can determine, adhesive matter is never derived from the pollinia, but is always rostellar in origin. Bentham (1881) restricted the term

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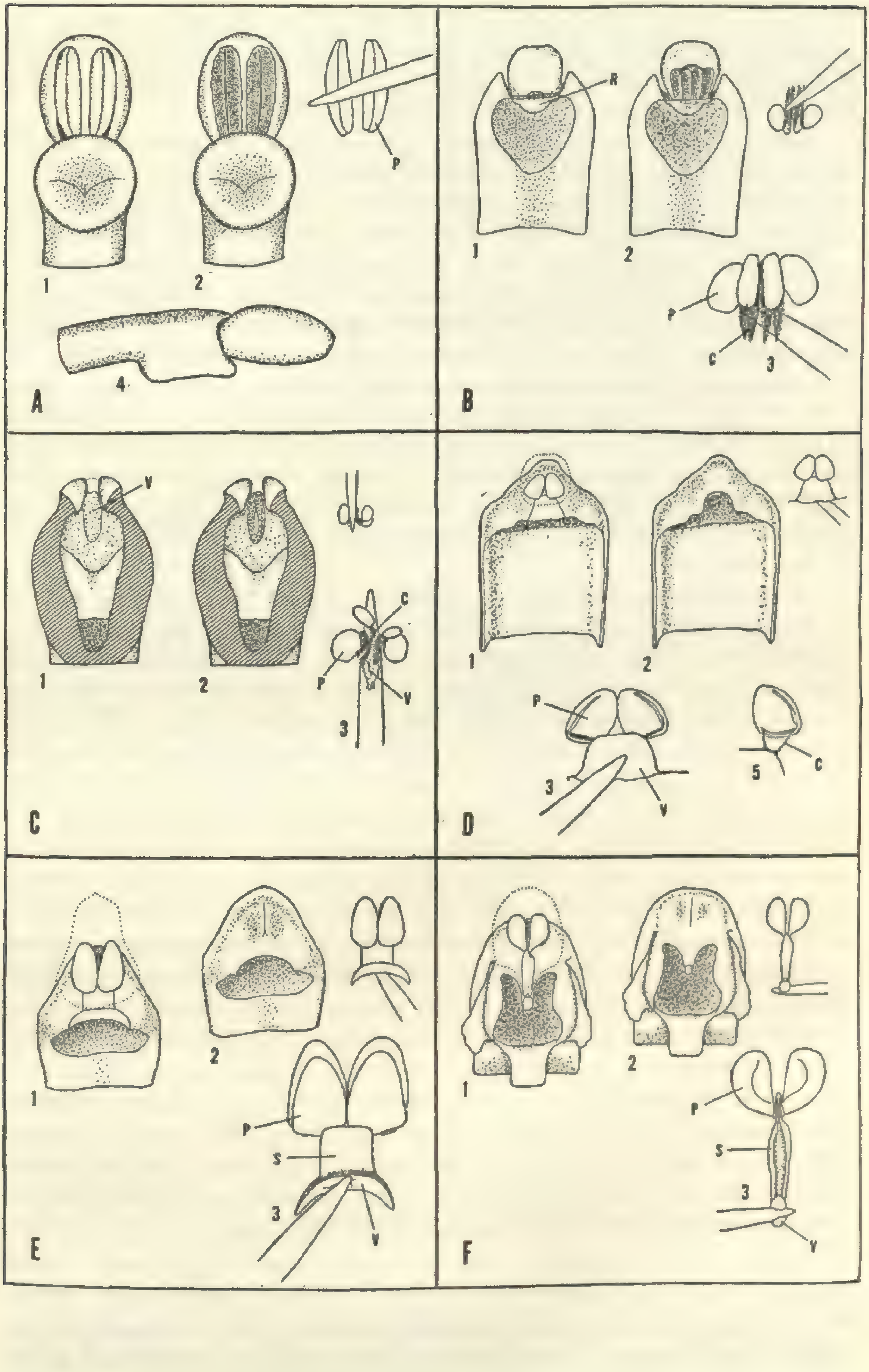
Figure 5. Examples of pollen apparatus found in the orchids. 1. The underside or apex of the column showing the stigma, and the pollinia in place within the anther. The anther is shown by dotted lines in C–F. 2. Same with the pollinia removed by a needle (to the upper right). 3. An enlarged view of the pollinia. c: caudicle; p: pollinia; r: rostellum; s: stipe; v: viscidium. A. *Cephalanthera rubra*: the anther is terminal and erect. Stigmatic fluid serves to attach the pollinia to insects, but no rostellum is differentiated. The pollinia are mealy. 4. Lateral view of column. B. *Cattleya aurantiaca*: the anther is operculate and versatile. A part of the stigma is specialized as the rostellum, but there is no direct connection between the pollinia and the rostellum. Well developed caudicles are present. C. *Epidendrum schlechterianum*: the anther is dorsal (and scarcely visible from beneath). A distinct, though semi-liquid viscidium is formed, and is attached directly to the caudicles of the pollinia. D. *Cymbidium lowianum*: a well developed viscidium is present, but no stipe. The four superposed pollinia are united into two. 5. pollinium slightly separated from viscidium to show the stretched caudicle. E. *Maxillaria elatior*: a short stipe is present but is not sharply differentiated from the viscidium. The four pollinia are superposed. F. *Oncidium anthocrene (powellii)*: a long stipe is present and sharply differentiated from the viscidium (the stipe is translucent at the point of attachment). This last represents a highly evolved pollen apparatus comparable to the structure found in *Asclepias*. All drawn from living material, except A, which is semi-diagrammatic and adapted from Godfery (1933) and Reichenbach (1851). A: ca. 5.5×. B, C & F: ca. 4.5× & 9×. D: ca. 2× & 3.5×. E: ca. 3.5× & 6.5×.


A
B
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caudicle to the tribe Orchideae, and used "appendage" for the mealy portion of the pollinia of the Epidendreae. This distinction is taxonomic rather than morphological, and generally has not been followed by other botanists. There is a clear morphological distinction, though, between stipe and caudicle.

Several trends of specialization occur in the pollinia of the Epidendreae, and all may be derived from the subclavate pattern found in many Bletiinae (see fig. 4). In the Pleurothallidinae, *Glomera, Podochilus* and some sections of *Eria,* the pollinia are strongly clavate. Within these groups reduction to four or even two pollinia occurs in several cases (ex. in the Pleurothallidinae). Viscidia are relatively frequent (*Glomera, Podochilus,* some Pleurothallidinae, *Meiracyllium,* etc.). Stipe-like structures are found in the *Podochilus* alliance, but these may be caudicular in nature, as are those of the Thelasiinae, according to Mansfeld (1937b). In *Dendrobium* and *Bulbophyllum* the four pollinia (which are probably derived from a clavate pattern) are quite naked; the versatile anther, however, is well designed to bring the pollinia in contact with the rostellar adhesive. In the Genyorchidinae and Thecostelinae both a viscidium and a stipe-like structure are formed. The close affinity of *Bulbophyllum* suggests that the Genyorchidinae may lack caudicles. If this is the case, the pollinia must be attached to the viscidium by true stipes, as they appear to be.

In the *Epidendrum* and *Polystachya* alliances, some Bletiinae, and some sections of *Eria,* the pollinia are laterally flattened and usually more or less discoid. The primitive pattern here appears to be that found in *Laelia, Brassavola,* and some species of *Bletia.* In these genera the pollinia are relatively discoid, and each pair is connected by a conspicuous caudicle, which may be about as long as the anther cell. The simplest modification of this pattern is the reduction or complete loss of the terminal pollinium in each set. Thus the pattern of *Cattleya, Epidendrum,* etc. is achieved, in which only four laterally flattened pollinia are formed. In these genera each pollinium bears a well developed caudicle which projects downward to the vicinity of the rostellum. In several genera, such as *Neobenthamia, Sophronitis* and *Epidendrum,* a small or ill-defined viscidium is formed, which is attached to the pollinia by means of the caudicles. In *Polystachya* and some species of *Epidendrum* the viscidium is quite well developed. In some species of *Polystachya,* such as *P. masayensis,* a distinct stipe is formed. Some other species, however, lack a stipe, and the close affinity of *Stolzia* and *Neobenthamia* clearly align *Polystachya* with the Epidendrinae. Reduction or fusion to two pollinia is infrequent in this series, but occurs in *Epidanthus* and some species of *Polystachya.* Also infrequent is the formation of superposed rather than laterally flattened pollinia. In some species of *Polystachya,* there appears to be a phyletic torsion which could lead to superposed pollinia. Semi-spherical, non-flattened pollinia occur in some species of *Epidendrum* and closely allied genera.

One of the most important trends is the development of superposed (rather than laterally flattened) pollinia, which are usually attached to a viscidium. While we have suggested that this pattern might be derived from the clavate pattern, further study is needed. The Collabiinae and Coelogyninae would seem to be

especially critical in this respect. Fusion of the four pollinia into two is common in this pattern. Holttum has suggested that division of two into four may occur in the Sarcanthinae. The fusion into four is frequently imperfect, and it is not unlikely that the trend may be reversed in some groups. Superposed pollinia are

PRIMITIVE	ADVANCED
Roots fleshy, without velamen	Roots spongy, with velamen
Rhizome slender, subterranean	Rhizome fleshy, epiphytic, or absent
Growth sympodial	Growth monopodial
Stem slender, elongate	Stem fleshy, or otherwise modified
Corms or pseudobulbs of many internodes	Pseudobulbs of a single internode
Leaves many, scattered, spiral	Leaves few, clustered or distichous
Leaves plicate	Leaves conduplicate
Leaves non-articulate, persistent	Leaves articulate, deciduous
Leaves herbaceous or leathery	Leaves fleshy
Inflorescence terminal	Inflorescence lateral
Lip similar to the other petals	Lip variously modified, unlike the petals
Flower without a spur	Flower with a spur or spurs
Filaments and style only partially united	Filaments and style completely united
Lateral anthers present and fertile	Lateral anthers staminodia or absent
Anther erect	Anther incumbent, or otherwise modified
Pollen soft, granular	Pollen variously united into pollinia, hard
8 waxy pollinia	Pollinia 6, 4 or 2
Rostellum absent, or simple, without a viscidium	A clearly defined portion of the rostellum (viscidium) removed with the pollinia
Pollinia without a distinct rostellar stipe	Pollinia with a distinct stipe
Ovary 3-celled	Ovary 1-celled
Seed with endosperm	Seed without endosperm
Seed with a wing or sclerotic testa	Seed with thin, reticulate coat

A chart comparing some of the primitive and advanced features to be found among the living orchids. A number of other specializations, such as saprophytism, sensitive anther, united sepals, etc., could be added. In some cases generally primitive features, such as non-articulate leaves or a simple lip, may occur among highly specialized groups. These features are not necessarily primitive in such cases, but may be secondary modifications. Some features are taken from Swamy (1949).

nearly always accompanied by a distinct viscidium (not so in *Coelogyne*). In the majority of genera from the Cyrtopodiinae to the Oncidiinae (as listed on p. 29), the rostellar tissues are differentiated into a distinct stipe which connects the viscidium to the pollinia. In *Cymbidium* and some Cyrtopodiinae and Maxillariinae, however, the stipe is absent or very small, so that it is difficult to separate the "Vandeae" on the basis of the stipe alone. The stipe may be partially or completely divided into two, as in *Dipodium* or some species of *Angraecum*. Even when a distinct stipe is present in these genera, it is usually connected to the pollinia by small caudicles. In *Oncidium*, *Cymbidium*, and others, the caudicle is concealed within the furrow formed by the incomplete fusion of the pollinia, and is readily seen only when stretched (fig. 5D).

Tribal Relationships and Phylogeny

With the possible exception of the Neottieae, the currently recognized tribes of orchids are relatively natural groups, whose genera are closely knit by clear interrelationships. The relationships between the tribes are less obvious; divergence and extinction apparently have been more important at this level. This is not to imply that the relationships between the tribes are extremely distant. The resemblances between *Tropidia, Apostasia, Palmorchis, Selenipedium* and *Cephalanthera* are strong enough that one may seriously doubt the advisability of distinguishing subfamilies within the Orchidaceae.

The relative advancement of the orchid tribes and their presumed relationships are schematically shown in figure 6. Since the relationships within the Neottieae are not altogether clear, we have diagrammed four different groups of this tribe separately. These are the groups as listed on p. 29. The Neottiinae and Spiranthinae are each treated separately, while the Diuridinae, Cryptostylidinae and Prasophyllinae are treated as one series of interrelated subtribes, and the remaining subtribes are grouped with the Limodorinae.

None of the living tribes of orchids could readily be derived from another living tribe, but their derivation from similar or common ancestors is easily visualized. The Cypripedieae are not very closely related to any other group, their relationship to the Limodorinae being perhaps quite as marked as their few resemblances to the Apostasieae. The ladyslippers have clearly diverged early from the main lines of orchid evolution. The Apostasieae more nearly approach the hypothetical ancestral type, the median anther being functional in *Neuwiedia*. They, too, represent a small relic group of somewhat isolated phyletic position, though perhaps closer to the other orchids than are the Cypripedieae. The Orchideae are presumably derived from somewhat *Cephalanthera*-like types, but they would stand quite isolated if it were not for the relic Epigoniinae, which show some relationships to both the Neottieae and the Epidendreae. The Epidendreae might be derived from somewhat Neottieae-like ancestors, but they show more primitive seed structure in the Vanillinae than any living Neottieae, and the two tribes have apparently diverged at an early level in orchid evolution. The subtribes of Neottieae which we group with the Limodorinae are among the more generalized and

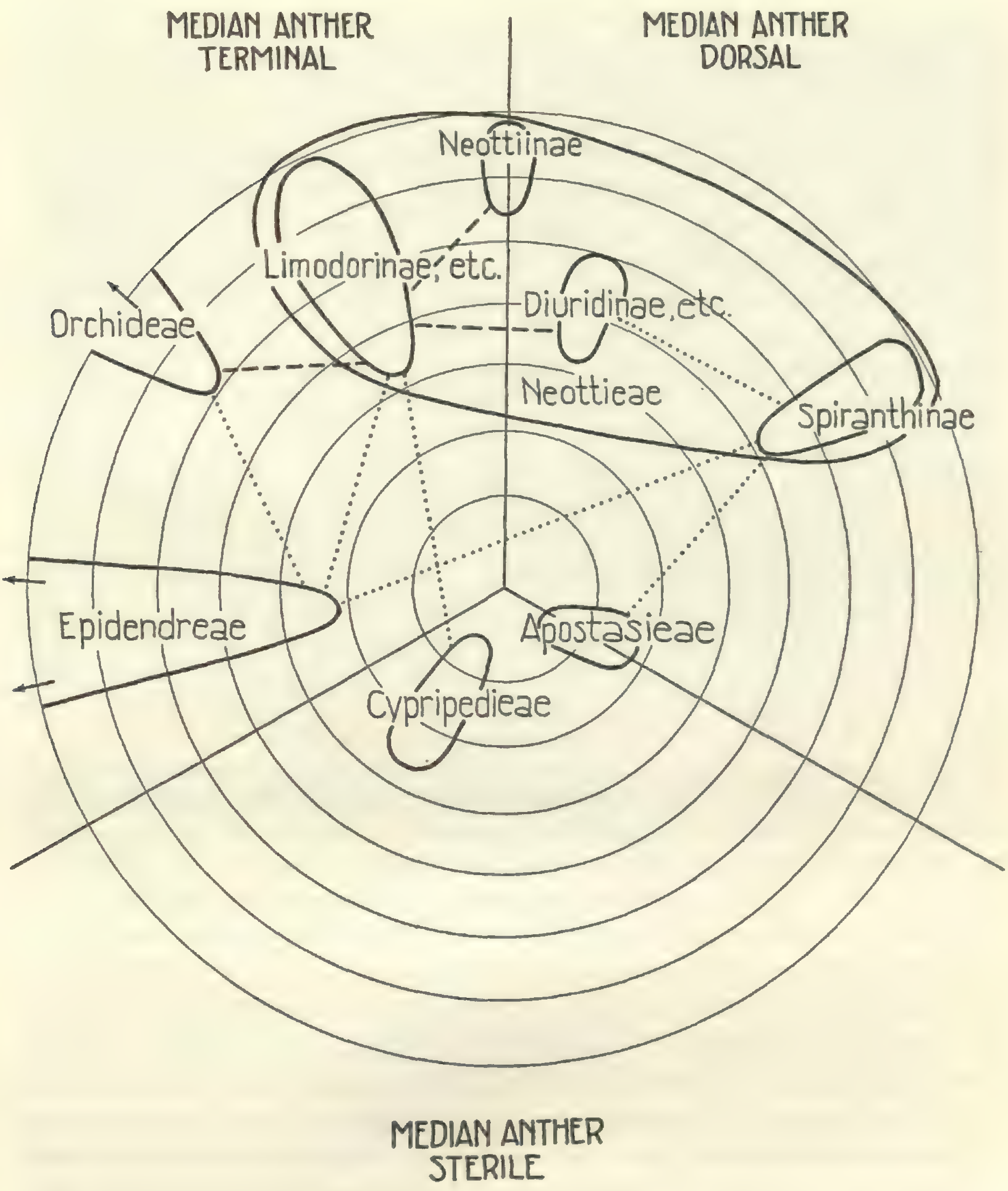

Figure 6. Relative advancement and suggested relationships among the orchid tribes. The less advanced groups have their bases nearer the center, and the ancestral type would fall within the central circle. A more complex advancement index would exclude the Cypripedieae from this sector. Dashed lines are meant to represent closer or more obvious relationships than dotted lines. The subtribes Neottiinae and Spiranthinae of the Neottieae are shown separately; the subtribes Diuridinae, Cryptostylidinae and Prasophyllinae are grouped together, while the remaining subtribes are grouped with the Limodorinae. The advancement index is calculated as follows: lateral anthers fertile, column incompletely formed, anther erect, pollinia mealy, ovary 3-celled, and seed with sclerotic coat or wing; each 0. lateral staminodia present, a distinct column formed, anther incumbent or reclinate, pollinia sectile or ceraceous, ovary 1-celled, and seed coat thin and reticulate; each 1 point. lateral stamens completely absent; 2 points.

primitive of the living orchids, and would be a typically relic group if it were not for the great evolution of this group in Australia, where several striking specializations occur. The association of the rostellum and the pollinia is usually basal or ventral (to the pollinia) in this group, but it is subterminal or quite terminal in a few cases. In the genus *Thelymitra* one finds a series from clearly ventral viscidia to some species with the viscidium quite terminal. There are some resemblances between *Thelymitra* and the Prasophyllinae, and these may indicate the derivation of the Prasophyllinae, Diuridinae, etc. from forms with a terminal, erect anther. On the other hand, the conspicuous, nearly free staminodia, and the slight union of filament and style in *Diuris* suggests a highly primitive condition not to be found in *Chloraea*- or *Caladenia*-like plants. The position of the anther in the Neottiinae is somewhat variable, but this subtribe seems most closely allied to the Limodorinae. In the Spiranthinae the anther is distinctly dorsal and does not overtop the stigma. In several genera the column is more theoretical than real, the short filament being only basally attached to the style (see, for example, Vermeulen's recent figure of *Goodyera,* 1959 p. 339). The *Tropidia* alliance, especially, bears a close resemblance to the Apostasieae. *Tropidia* has actually been described as a new genus of the Apostasieae by Gagnepain (see Mansfeld, 1934). In the absence of clear relationships between the Spiranthinae and other subtribes of the Neottieae, their position is unclear, and it is possible that they are not derived from forms with a terminal anther, but that the anther is primitively dorsal in this group.

The relationships which we suggest between the primitive members of the several orchid tribes are yet somewhat speculative. This is the level at which relationships are expected to be least clear, and, further, many of these orchids are poorly known. We have no detailed morphological information on the Apostasieae, for example. When more information is available on these plants, their interrelationships will surely be better understood, and we will be able to speculate on their origins with a much firmer basis. While the orchids are unusually favorable for a study of relationships within the family, we may never be able to build an exact and detailed family tree for the early evolution of the group.

We have suggested a change in the circumscription of the Epidendreae, which seems to render the group more natural from the phyletic standpoint and more definable from the descriptive standpoint. In a similar fashion it might possibly be desirable to separate the Spiranthinae as a separate tribe, but further study of this complex is needed. With reference to the subfamily Cypripedioideae, it may be that the Apostasieae should be given subfamilial rank, as Wettstein has already suggested, or it may be that the subfamilial division should be abandoned altogether. Another possibility which must be considered is the recognition of five subfamilies (as Brieger has already suggested, 1958) and the delineation of 10–12 tribes. Such a system might be more comparable to the classifications used for other major families (such as the Compositae and Gramineae).

In dealing with the primitive orchids and their evolution from groups now extinct, we must bear in mind the bewildering parallelisms to be found in the more

advanced groups. If all the monopodial genera with a distinct polliniar stipe were at hand and their sympodial allies extinct, no one could seriously doubt that he was dealing with a "natural" group. The separate and parallel evolution of the different genera of leafless Sarcanthinae would be inconceivable if we did not have the evidence at hand in their living relatives. It is altogether possible that the subfamily Orchidoideae, as now delimited, has not evolved from a single species which possessed all the features of the modern subfamily: column, single fertile anther and rostellum. Rather, this group has probably evolved from a series of related species or genera with partial union of filaments and style, androecial zygomorphy and a close association of the stigma and the median anther; all features which would predispose the group to parallel patterns of evolution. Some of the ancestral populations may have been quite similar to the Apostasieae, while others were similar to *Selenipedium*, and yet others quite unlike either. The orchid family is not "unnatural" or polyphyletic in the strict sense, since the ancestral group was, itself, a natural and closely interrelated group, even though it may have differed from the modern orchids in a number of features. We feel fairly sure that the stipe, sectile pollinia and the viscidium have evolved independently in different groups of orchids. It is quite possible that the rostellum, itself, has evolved independently in two or more separate lines and that the reduction to a single median anther is similarly polyphyletic in the unusually "natural" family Orchidaceae.

The patterns of phylogeny and relationships within the orchid tribes help us to understand the evolution of the tribes themselves. A better understanding of both levels may throw more light on the patterns of origin for families and higher categories.

Discussion and Conclusions

Probably the foremost conclusion to be reached from a survey of orchid classification is that there are no infallible "key characters." The habit of growth, the presence or absence of pseudobulbs, the nature of the leaves, the position of the inflorescence, the presence or absence of a column foot, the texture of the pollen, the number of pollinia, and the presence or absence of viscidium or stipe; all have been assigned great importance in orchid classification. Yet in every case one can find closely related species which differ in the feature chosen, or even, in some cases, variation within a species. This lack of hard and fast key characters does not mean that a classification of the orchids is impossible. It does mean that a classification must be based on all features of the plant and that comprehensive keys will often be difficult to prepare. Students of the orchids have often erred in assigning too great importance to a single feature. Both our systems of classification and our concepts of relationship are based on relatively few features. With intensive systematic and morphological study we will be able to base our systems on a much broader and firmer foundation.

Ames (quoted by Schweinfurth, 1959) has suggested that many of the difficulties in orchid classification are due to extinction. We feel, on the contrary, that a relative lack of extinction characterizes the family. Interfertility between

morphologically very distinct genera and close morphological resemblances between subtribes, tribes and even subfamilies point to a rapidly evolving group in which extinction has played a minor role. The groups of orchids are closely interrelated, and clear indications of phylogeny are often to be found. Parallelism also plays a part in rendering orchid classification more difficult. There is every indication that monopodial growth, saprophytism, compact pseudobulbs, conduplicate leaves, lateral inflorescences, spurs, viscidia, stipes, and reduction in number of pollinia have all occurred independently in two to several different groups of orchids. It is difficult to define clearly the several groups of monopodial orchids with highly evolved pollinia, yet there appears to be no direct relationship between them. Both classification and phylogeny must be studied by tracing relationships from group to group.

As a family undergoing relatively rapid evolution, the Orchidaceae provide excellent material for the study of evolution. A chart of primitive and advanced features is given on p. 61; a scheme showing the probable relationships between the tribes in fig. 6. There is a tendency to define the family Orchidaceae in terms of its specializations (such as the column, rostellum or pollinia), but one must not lose sight of the primitive features to be found in living orchids. The style and filment are partially free in both the Apostasieae and the Diuridinae; the pollen grains are free in the Vanillinae, and the seeds possess a thick, sclerotic testa in this same subtribe. *Cephalanthera* lacks a rostellum, and several genera bear an erect, relatively unspecialized anther. The patterns of evolution within the family point rather clearly to an ancestor which would be classified in the Lilialean complex of living monocotyledons. Hutchinson has specifically suggested the Hypoxidaceae as a possible close relative of the Orchidaceae. Further morphological study of the primitive orchid genera may greatly clarify this problem. There is no direct relationship between the orchids and the Zingiberales, but rather striking parallelisms, as Hutchinson has suggested. The supposed relationship between the Orchidaceae and Burmanniaceae is based primarily on the tiny seeds; but this type of seed is to be expected in any saprophytic group, and the floral symmetry and inflorescence are basically different in the two groups (Jonker, 1938).

Not only are the fleshy flowers of many orchids crushed in the preparation of herbarium specimens; several of the parts considered important in classification (viscidium, caudicle, pollinia) are frequently dissolved by either alcohol or water. The study of living plants is, thus, especially important. Orchids can, of course, be identified from dried specimens, but a better understanding of relationship is to be obtained from the living plant. Field work by specialists cannot fail to add greatly to our knowledge, while the great variety of orchid genera cultivated by hobbyists can be of great value to botanists.

Finally, we must stress the limitations of the present paper. We have reviewed the nomenclature of orchid tribes and subtribes, following the rules of botanical nomenclature, including priority. We have attempted to evaluate the system of Schlechter, and have offered several changes in arrangement and circumscription, as well as a key to the subtribes which we recognize. We do not consider this a

final, complete system of orchid classification, so much as an evaluation of previous systems, and a working system to be improved and replaced as soon as possible. A discussion of several aspects of orchid phylogeny is presented. Many of the problems which are raised here can best be studied by regional specialists, and it is hoped that the present paper may stimulate such research.

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THE GENUS SCHISMATOGLOTTIS (SECTION PHILONOTION) IN AMERICA

GEORGE S. BUNTING

ABSTRACT

The genus *Philonotion* Schott is included in *Schismatoglottis,* forming the American section of an otherwise Asian group. Two species are recognized in this section: 1) *S. americana,* known only from Surinam, and 2) S. **spruceanum**, here transferred from the genus *Philonotion* and represented by two varieties: var. *spruceanum* of Amazonian Venezuela and adjacent Colombia, and var. **williamsii** of Amazonian Venezuela only. GEORGE S. BUNTING, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

The genus *Philonotion* was published by Schott (Gen. Aroid. 54. 1858.) to accommodate a single Spruce collection from Amazonian Brazil. For a century, this monotypic genus has been maintained and included in various works on the Araceae. Known from the type collection only, its alliance was variously interpreted. Schott (Prod. Syst. Aroid. 317. 1860.) judiciously placed *Philonotion* in the subtribe Adeloneminae immediately preceding subtribe Schismatoglottidinae. Engler (Pflanzenreich IV. 23(55):24. 1912.) included it in the subtribe Philodendrinae following *Philodendron.* This latter treatment is curious, since that author noted the parietal placentation, the distinctive stamens with apical pores, and the non-scandent habit of growth of *Philonotion.* In contrast, placentation in *Philodendron* is axile, the stamens are of an entirely different nature, and the species are predominantly scandent. The deciduous nature of the blade of the spathe and staminate portion of the inflorescence after anthesis in *Philonotion* further differentiate these two genera.

Philonotion falls clearly into the subtribe Schismatoglottidinae as defined by Engler (l.c. p. 24). Indeed it appears that *Philonotion* is the American section of the otherwise Malaysian genus *Schismatoglottis.*[1] The first and only American species to be described in the latter genus is *S. americana* Jonk. & Jonk. Following its description (Acta Bot. Neer. 2(3):362. 1953.), the authors commented upon the apparent relationship between *Philonotion* and *Schismatoglottis.* The current study has verified the close affinity of these two genera, and has demonstrated clearly that *S. americana* is congeneric with material referred by other workers to *Philonotion.*

Philonotion was initially characterized by a unilocular ovary bearing one parietal ovule. Recent collections that are undoubtedly conspecific with the type of this genus (*P. spruceanum* Schott) have either one or two parietal placentae each bearing one or two ovules, and the unilocular ovary may thus contain one to four ovules. The Malaysian *Schismatoglottii* commonly have ten or more ovules per ovary attached along three parietal placentae. With the exception of the fewer ovules, however, there is no constant floral character separating *Philonotion* from *Schismatoglottis.* Generally, an occasional staminode is found among the pistillate

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[1] Similar disjunction exists in other aroid genera. *Homalomena* is a predominantly Asian genus of about eighty species, six or seven of which occur only in America and have characters diverse enough to be considered as a separate section of the genus by Engler. A similar disjunction occurs in the genus *Arisaema.* One species of the otherwise American genus *Spathiphyllum* is native in Indonesia and the Philippines.

flowers in the latter genus, and some species have a sterile appendage of the spadix. The American species, previously referred to *Philonotion,* exhibit neither of these characteristics, but rather possess one outstanding vegetative feature apparently not found in any Asian species—the aristate or subcaudate apex of the leaf blade. Despite these differences, it seems prudent to reduce *Philonotion* to the rank of section under *Schismatoglottis.*[2]

Schismatoglottis section **Philonotion** (Schott) Bunt. stat. nov.
Philonotion Schott, Gen. Aroid. t. 54. 1858.

Key to the Species

A. Leaf blade 2–2.5 times longer than wide, 9 cm. or more wide, elliptic to oblanceolate. ....1. S. americana

AA. Leaf blade narrower, 6 cm. or less wide, lanceolate to oblong.

B. Blade 3–5 times longer than wide, 2.5–6 cm. wide.......2a. S. spruceanum var. spruceanum

BB. Blade 7.5–9 times longer than wide, to 1.8 cm. wide.......2b. S. spruceanum var. williamsii

1. Schismatoglottis americana Jonk. & Jonk. Acta Bot. Neerl. 2(3):360, fig. 2. 1953.

holotype: *Maguire 24289,* Tafelberg, Surinam, Aug. 1944 (NY). Known only from the type collection.

2. Schismatoglottis **spruceanum** (Schott) Bunt. comb. nov.
Philonotion spruceanum Schott, Gen. Aroid. t. 54. 1858.

2a. Schismatoglottis spruceanum var. spruceanum.
Stenospermatium verecundum R. E. Schultes, Bot. Mus. Leafl. 18(4):121–122, pl. XXI, XXII. 1958.

lectotype: *Spruce 2948,* in ripis rivuli umbrosi, secus Panuré, Alto Amazonas, Brazil, Feb. 1853 (K). This is a duplicate of the holotype. The latter was deposited at Vienna and presumably destroyed when that herbarium burned following World War II. I have seen only a photograph of the Kew sheet; it appears to be nearly identical to the largest specimen on the New York sheet of *Maguire 36413.*

additional specimens: *B. Maguire, J. J. Wurdack, & G. S. Bunting 36311,* Yavita-Pimichín trail, Río Guainía, Terr. Amazonas, alt. 120–140 m., Nov. 21, 1953; *36413,* sabanita 1 km. east of Maroa, Río Guainía, Terr. Amazonas, Venezuela, alt. 120–140 m., Nov. 25, 1953; *36415A,* same data as *36413.*

The infrutescence of this variety has not been previously described. It is fusiform, about 3.5 cm. long and to 1.5 cm. in diameter (in the dried specimen), green, the apex more or less truncate (resulting from loss of blade of spathe), the

[2] To include this section, Engler's description of Schismatoglottis (Pflanzenreich IV. 23(55):82. 1912.) is emended as follows: " . . . placentis 1–4 parietalis e baseos adscendentibus; ovula 1–plura hemianatropa vel hemiamphitropa . . . ".

free upper margin revolute; fruits many, baccate, oblong, about 3 mm. long, 1 mm. broad, 1(–2)-seeded.

Schultes & Cabrera 17496 (GH), collected along Río Piraparaná, Comisarías del Amazonas & Vaupés, Colombia, appears to belong here. Unfortunately, that specimen could not be located at the time of this study. It is cited as type of *Stenospermatium verecundum*, but the photograph and plate accompanying the description of that species illustrates a plant clearly referable to *Schismatoglottis spruceanum.*

2b. SCHISMATOGLOTTIS SPRUCEANUM var. **williamsii** (Steyerm.) Bunt. comb. nov.

Philonotion williamsii Steyerm. Fieldiana Bot. 28(1):99, fig. 14. 1951.

HOLOTYPE: *L. Williams 13922,* Yavita, Terr. Amazonas, Venezuela, alt. 128 m., Jan. 23, 1942 (F).

ADDITIONAL SPECIMENS: *B. Maguire, J. J. Wurdack, & G. S. Bunting 36415B,* sabanita 1 km. east of Maroa, Río Guainía, Terr. Amazonas, Venezuela, alt. 120–140 m., Nov. 25, 1953. This is a mixed collection, *36415A* representing S. *spruceanum* var. *spruceanum.*

This variety appears to grow together with the variety *spruceanum,* but is distinctive in its much narrower leaf blades and slender petioles. Too few specimens have been collected to indicate to what degree these two forms intergrade.

S. *spruceanum* is a savannah species, occuring in partial sun on white sandy soil. It seems inappropriate to consider these conditions as "extreme xerophytism" as Schultes suggests (Bot. Mus. Leafl. 18(4):122. 1958.). Though the habitat may appear xeric, my field observations at Yavita and Maroa, Venezuela, were that abundant moisture was present about the roots of the plants.

MISCELLANEA TAXONOMICA. II.

ABSTRACT

The following new taxa are described—Amaryllidaceae: *Crinum* **brevilobatum** G. McCue; Loganiaceae: *Desfontainea* **costaricensis** Woodson; Apocynaceae: *Aspidosperma* **limae** Woodson, **Woytkowskia spermatochorda** Woodson, *Tabernaemontana* **brachyantha** Woodson, *Peltastes* **ampliflorus** Woodson, *P.* **peruvianus** Woodson, *P.* **tubiflorus** Woodson, *Mandevilla* **sandemanii** Woodson, *Prestonia* **caudata** Woodson; Asclepiadaceae: *Matelea* **rivularis** Woodson.

AMARYLLIDACEAE

CRINUM **brevilobatum** G. McCue, spec. nov.

Bulbus cylindraceus cr. 11.5 cm. longus. Folia 6 lorata acute acuminata 38–48 cm. longa 4.5–5.0 cm. lata stricte erecta nervis 36–46 parallelis in reticulo per venas breves transversas conjunctis margine denticulis minutis inaequalibusque inaequaliter positis. Pedunculus 27–47 cm. longus in statu compresso 2–4 mm. latus; bracteae 2 inter sese liberae paene vaginantes anguste ellipticae 8 cm. longae apice acutae; flores in umbella 2–4 sessiles v. subsessiles. Perianthii tubus 15–17 cm. longus in statu compresso usque 2–4 mm. latus erectus; limbi segmenta elliptico-lanceolata apice acuminata 3.5 cm. longa medio 5 mm. lata colore flos lactis. Stamina segmentis corollae breviora 1.2 longa prope faucem instructa; antherae lineares 1.2 cm. longae sub medio versus affixae. Stylus corolla perpaullo brevior; stigma minutum lobatum. Ovarium 1.2 cm. longum.

COSTA RICA: ALAJUELA: in moist humus at edge of forest along Río Frío, low tropical rainforest with palms prominent, vicinity of Los Chiles, alt. 30–40 m., August 1, 1949, *R. W. Holm & H. H. Iltis 695* (HOLOTYPE, MO).

This species is referable to subgenus PLATYASTER of Baker, but is remarkable for the short perianth segments relative to the greatly elongate tube.

LOGANIACEAE

DESFONTAINEA **costaricensis** Woodson, spec. nov.

Frutices epipytici; ramulis usque 1 m. longis crassiusculis subtetragonis valde compressis semper glabris maturitate cortice luteo-brunneo rimoso tectis. Folia opposita; lamina obovata 2–6 cm. longa 1.5–2.5 cm. lata basi anguste cuneata in petiolum 0.5–1.0 cm. longum decurrente supra medium prominente spinoso-dentata. Flores solitarii ramulos axillares perbreves terminantes; pedicello ca. 1.5 cm. longo; calycis laciniis ovato-ellipticis acutis ca. 6 mm. longis omnino glabris; corollae salverformis tubo paene recto ca. 2 cm. longo basi ca. 2.5 mm. diam. fauces versum paulo ampliato aurantiaco-rubeo, lobis late ovatis ca. 8 mm. longis paulum patulis luteis.

COSTA RICA: CARTAGO: dense virgin cloud-forest, vicinity of Millsville, Pan-American Highway, about 3 km. above Nivel, alt. 3000–3300 m., July 22, 1949, *R. W. Holm & H. H. Iltis 534* (HOLOTYPE, MO).

An interesting addition to the flora of Central America, this species approaches *D. obovata* Krzl., of Peru, in the small calyx which, however, is ciliate as is usual in

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the Andean species. There probably is close relationship also to *D. pulchra* Moldenke, of Venezuela, which, however, has oblanceolate subentire leaves.

APOCYNACEAE

Aspidosperma limae Woodson, spec. nov.

Arbores altae sicut collector dixit altitudine ignotae laticem sanguineum exudentes; ramulis pro magnitudine graciliusculis glabris vel juventate minutissime papillatis cortice atrofusco arcte compresso. Folia irregulariter approximata longe petiolata; lamina latiuscule elliptica apice valde acuminata basi obtuse cuneata ca. 8–12 cm. longa 3.5–5.0 cm. lata rigide coriacea margine paulo revoluta supra valde illustri colore olivacea venis immersis subtus pallidiore venis vix bene visis utrinque glabra; petiolo 2–4 cm. longo tenui glabro colore ramuli. Inflorescentiae terminales et subterminales manifeste cymosae; ramulis terminalibus quam lateralibus conspicue brevioribus sordide griseo-tomentellis multifloris foliis subaequantibus; bracteis vix bene visis; pedicellis vix 1 mm. longis. Calycis laciniae ovate acutae 2 mm. longae atrogriseo-tomentellae. Corolla luteola extus glabra; tubo valde angulato ca. 3.5 mm. longo 1.5 mm. lato; lobis ca. 3.5 mm. longis valde caudato-acuminatis et spiraliter contortis. Folliculi magni oblique elliptico-ovales apice late obtusi basi in stipitem crassum sensim producti 15–18 cm. longi 8–9 cm. lati dense fuscogriseo-tomentelli; seminibus late ovalibus ca. 8 cm. longis 7 cm. latis.

Brasil: pernambuco: Recife, Dois Irmãos, Oct. 4, 1949, *Dárdano de A. Lima 49-333* (holotype, MO).

This very distinct species of series nobiles will key in my revision of *Aspidosperma* (Ann. Missouri Bot. Gard. 38:185. 1951) to the alliance of *A. album* and *A. sandwithianum* because of the inflorescences of distinctly cymose aspect (the determinate branches much shorter than the divaricate lateral branches). However, the general aspect of the specimens is much more reminiscent of *A. megalocarpon,* particularly because of the massive densely tomentellous follicles. It is the first species of series nobiles recorded for Pernambuco. Mr. Lima quotes the popular name of the trees as *pitía marfim* and states that the timber is useful for cabinet work.

Woytkowskia spermatochorda Woodson, gen. et spec. nov. *(Tabernaemontanoideae)*

Frutices mediocres lactescentes. Folia disticha anisophylla; lamina obovato-elliptica abrupte caudato-acuminata basi latiuscule cuneata ca. 9–20 cm. longa 5–9 cm. lata tenue membranacea glabra nervis secundariis in utroque latere 10–16 arcuatis; petiolo 5–12 mm. longo basi paulo amplectanti et in axilla pluriglanduloso. Inflorescentia aut terminalis aut interpetiolaris cymosis subtriflora. Flores gilvi pedicellati; calycis laciniis 5 subaequalibus late ovato-deltoideis rotundatis 3–4 mm. longis glabris intus in axillis pluriglandulosis; corollae tubulo-salverformis tubo conico-cylindrico ca. 2.0–2.5 cm. longo basi ca. 4 mm. diam. ostio ca. 1.5 mm. diam extus glabro, lobis 5 ante anthesim in ostium fere omnino inflexis

Figure 1. *Woytkowskia spermatochorda* Woodson

(alabastro apice manifeste invaginato) oblique oblongis ca. 5–6 mm. longis; antheris 5 sessilibus anguste sagittato-lanceolatis ca. 11 mm. longis basibus thecarum paulum incurvis angustis sterilibus medio tubo corollae insertis; carpellis pistilli 2 apocarpis oblongo-ovoideo in quoque loculo ovulis multis 2-seriatis, stylo gracili, stigmate umbraculiformi parte apicali anguste bifida parte media dilatata subglobosa leviter sulcata basi contracta parte basali limbo brevi reflexo, nectario annulari demisso carnoso subintegro. Folliculi 2 lineari-fusiformes usque 20 cm. longi 5 mm. lati pericarpio sicco tenui extus indistincte striato glabro; seminibus late fusiformibus ca. 8 mm. longis testa fusca profunde striata arillo sicco papyraceo ca. semi-involutis placenta filiformi decidua persistente affixis.

Peru: loreto: in forest, Aguaytia, alt. 300 m., F. *Woytkowski 5338* (holotype, MO).

The fruits are utterly unlike those of any *Tabernaemontana* known to me. Whilst the seeds are provided with the aril common to the alliance, here it is dry and not fleshy, being permanently attached to the peculiar filiform deciduous placenta from which the specific substantive is coined. The elongate follicles also are unparalleled in Tabernaemontanoideae.

The corolla lobes of *Tarbernaemontana* ordinarily are partially included within the throat prior to anthesis; but here they are almost completely inflexed, rendering the tip of the bud decidedly concave. I have only unopened buds available for examination, but assume that the lobes are extruded from the orifice at anthesis.

The specific epithet descriptive of the placenta might be used more strikingly as a generic name, but I feel constrained to commemorate in this way the invaluable botanical contributions of my colleague Félix Woytkowski.

Tabernaemontana **brachyantha** Woodson, spec. nov.

Frutices altitudine ca. 3 m.; ramulis teretibus fuscis glabris vel indistincte papillatis. Folia disticha subisophylla; lamina late ovato-elliptica subcaudato-acuminata basi obtusa 15–25 cm. longa 5–12 cm. lata membranacea glabra subtus subglauca nervis secundariis in utroque latere 15–20 arcuatis; petiolo 1–2 cm. longo basi paulo amplectanti et conspicue elevato-mitrato in axilla pluriglanduloso. Inflorescentia aut terminalis aut interpetiolaris dichotome cymosa ca. 20-flora petiolis paulo superans. Flores pro genere parvi albi breviter pedicellati. Calycis laciniae ovate late acutae similes ca. 2 mm. longae minute ciliolatae in axillis squamellis ligularibus 4–6 gerentes. Corollae salverformis extus glabrae tubo cylindrico 9–10 mm. longo basi ca. 1.5 mm. diam. ostio paulo constricto, lobis limbi oblique oblongo-ovatis ca. 4 mm. longis post anthesim patulis in alabastro ca. dimidio inclusis. Antherae sessiles vix inclusae 3 mm. longae caudiculis sterilibus paululo incurvis. Pistilli carpelli ovoideo-fusiformia glabri intus ovulis multis 2-seriatis, stylo gracili, stigmate ca. 1 mm. diam. parte apicali minute 2-dentata media oblate 5-gona basali limbo brevi reflexo, nectario 5-lobato adnato demisso. Fructus ignotus.

Peru: loreto: Aguaytia, in forest, alt. 300 m., May 10, 1959, F. *Woytkowski 5345* (holotype, MO).

I assume that this is a species of the *Bonafousia*-complex of *Tabernaemontana* (*sensu lato*) but the flowers are far smaller than for those of any other species known to me and furnish a striking contrast to the large leaves. The fruit should be awaited with unusual interest.

I feel that insufficient prominence has been given to the vegetative characters of the Tabernaemontanoideae—the dichotomous branching of the stem, the interpetiolar inflorescence, and particularly the inconspicuous prophyll which is the first-borne appendage of each dichotomous branch and by means of which alone the frequent "lateral" inflorescences may be demonstrated as terminal. The very base of the petioles is somewhat amplectant and canaliculate for the protection of the terminal bud, and not infrequently developed into a conspicuously elevated hood, as in this species.

Peltastes **ampliflorus** Woodson, spec. nov.

Frutices volubiles; ramulis teretibus crassis juventate minute ferrugineo-papillatis. Folia opposita petiolata; lamina peltata latissime ovata apice abrupte mucronata basi late rotundata 25–30 cm. longa 20–22 cm. lata firmiter membranacea supra glabra subtus pallidiori inconspicue ferrugineo-papillata; petiolo 6–7 cm. longo ferrugineo-tomentello. Inflorescentiae in axillis oppositis foliorum pluriflorae; pedunculis ca. 6–8 cm. longis ferrugineo-tomentellis; pedicellis 1.5–2.0 cm. longis minute ferrugineo-tomentellis. Flores infundibuliformes gilvi extus minute dense ferrugineo-puberuli; calycis laciniis valde inaequalibus interioribus oblongis ca. 1.8 cm. longis exterioribus late ellipticis ca. 2 cm. longis omnibus foliaceis extus dense puberulo-papillatis; corollae tubo proprio ca. 1.5 cm. longo basi ca. 3 mm. diam., faucibus angustissime conicis ca. 4 cm. longis ostio ca. 1.2 cm. diam., lobis late dolabriformibus obtusis ca. 2 cm. longis 1.5 cm. latis patulis; antheris anguste sagittiformibus dorso glabris.

Peru: san martin: mountain forest, Zepelacio near Moyobamba, alt. 1100 m., August, 1934, G. *Klug 3754* (holotype, MO).

I had previously determined this specimen as *P. giganteus*, which cannot be accepted because of its glabrous anthers. It must be very closely related to *P. peruvianus*, but the ferruginous-puberulent corollas of somewhat different shape would appear to preclude that, as well as the larger broader foliage, smaller narrower calyx lobes, etc. The "new species" of *Peltastes* appear to be multiplying alarmingly, due mostly to myself, but the genus is encountered by collectors so infrequently that an adequate evaluation of the infra-specific variation seems impossible at present.

Peltastes **peruvianus** Woodson, spec. nov.

Frutices volubiles validi ca. 4–6 m. alti; ramulis teretibus crassiusculis juventate dense ferrugineo-tomentellis. Folia opposita longe petiolata; lamina peltata late ovali apice abrupte breviterque subcaudato-acuminata basi rotundata 20–25 cm. longa 14–16 cm. lata firmiter membranacea supra glabra subtus pallidiore praecipue in nervis minute ferrugineo-tomentella. Inflorescentiae in axillis oppositis

foliorum pluriflorae; pedunculis ca. 5–6 cm. longis minute tomentellis; pedicellis ca. 2 cm. longis ut in pedunculo vestitis. Flores infundibuliformes gilvi extus glabri; calycis laciniis inaequalibus late ellipticis apice acutis vel obtusis 2.0–2.5 cm. longis 0.8–1.0 cm. latis foliaceis; corollae tubo proprio ca. 1.2 cm. longo basi ca. 3 mm. diam., faucibus subtubiformibus vel angustissime campanulatis ca. 3 cm. longis ostio ca. 1 cm. diam., lobis patulis latissime dolabriformibus apice anguste acutis ca. 2.5 cm. longis et latis; antheris anguste sagittiformibus dorso glabris. Fructus ignoti.

PERU: HUANUCO: on outskirts of forest, alt. 1600 m., Divisoria, Sept. 6, 1946, *F. Woytkowski 34492* (HOLOTYPE, MO).

The glabrous anthers ally this species and the preceding with *P. malvaeflorus* of southeastern Brazil and *P. stemmadeniiflorus* of Paraguay, from both of which it is distinguished by the exceedingly short proper tube and the very narrow throat of the corolla. Isotypes may be found labeled as *Macropharynx* in other herbaria.

PELTASTES **tubiflorus** Woodson, spec. nov.

Frutices volubiles validi; ramulis florigeris crassiusculis teretibus dense minuteque ferrugineo-tomentulosis. Folia basi peltata obovato-ovalia apice breviter cuspidata basi rotundata 15–20 cm. longa 9–12 cm. lata membranacea utrinque dense minuteque ferrugineo-tomentulosa supra glabrata; petiolo 4–5 cm. longo. Inflorescentiae in axillis foliorum binis corymbose fasciculatae pluriflorae omnino minuteque ferrugineo-tomentulosis petiolis breviores. Flores pro genere perparvuli. Calycis laciniae foliaceae late oblongo-lanceolatae acutae ca. 1.5–1.7 cm. longae, squamellis multis dentiformibus. Corolla tubulo-salverformis, tubo 5-gono ca. 1.8 cm. longo basi ca. 3–4 mm. diam. dein paulo ampliato prope medio abrupte constricto ibique staminigero deinde ampliato deinde ad ostium ca. 2 mm. diam. gradatim angustato, lobis patulis oblique ellipticis ca. 1 cm. longis. Anthera sagittata more generis ca. 8 mm. longa dorso glabra. Ovarii carpella late ovoidea ca. 1.5 mm. longa glabra basi nectriis 5 humilibus cincta.

BRASIL: MINAS GERAIS: Fazenda Varginha, 12 km. E. of Ponte Nova, Municipio Ponte Nova, 7 December 1958, *H. S. Irwin 2246* (HOLOTYPE, US).

The corolla of all other species is far larger and broadly infundibular. Another *Peltastes* sent me for identification by the U. S. National Herbarium at the same time as the above is *Kuhlmann 2528* from Viçosa, Minas. It apparently also has small flowers much like those of the Irwin number, but is not in condition for close examination. I hesitate to assign it to *P. tubiflora* because of its definitely ovate leaves with a more minute scarcely ferruginous indument.

MANDEVILLA **sandemanii** Woodson, spec. nov.

Frutices volubiles vel subvolubiles; ramulis crassiusculis juventate dense fulvo-tomentulosis. Folia opposita breviter petiolata; lamina ovata vel ovato-elliptica apice late acuta minuteque mucronulata basi late cordata ca. 11 cm. longa 5–6 cm. lata membranacea utrinque fulvo-tomentulosa subtus densius nervo medio basi pauciglandulosa; petiolo 1.0–1.5 cm. longo dense tomentuloso. Inflorescentiae

axillares simplice racemosae in holotypo laxe 17-florae; pedunculo 35 cm. longo crassiusculo; pedicellis sat distantibus ca. 3 cm. longis ut in pedunculo minute fulvo-tomentulosis; bracteis minutis vix bene visis. Flores spectabiles; calycis laciniis ovato-lanceolatis anguste acutis 8–9 mm. longis foliaceis conspicue puberulis; corolla infundibuliformis viridi extus glabra, tubo proprio cylindrico ca. 2 cm. longo basi 2 mm. diam., faucibus campanulatis ca. 1.3 cm. longis ostio ca. 1 cm. diam., lobis fere erectis late dolabriformibus minute apiculatis ca. 2.5 cm. longis 1.3 cm. latis; antheris anguste elliptico-oblongis basi truncatis ca. 1 cm. longis dorso glabris; carpellis ovoidio-oblongoideis, ca. 2 mm. longis glabris, nectariis 5 distinctis subquadratis subaequalongis, stigmate umbraculiformi conspicue apiculato. Fructus ignoti.

PERU: HUANUCO: Carpish divide, alt. 9000 ft. alt., Oct. 7, 1945, *C. Sandeman 5154* (HOLOTYPE, K).

Mandevilla sandemanii is most closely related to *M. alboviridis* which is known only from the type specimen from Colombia. The flowers (as well as the whole inflorescence, for that matter) of the former is very much larger in all respects, however, and the nodes are without the conspicuous coriaceous appendages which distinguish the latter.

PRESTONIA (§ COALITAE) **caudata** Woodson, spec. nov.

Frutices volubiles graciles glaberrimi; ramulis teretibus striatis subglaucescentibus, internodiis elongatis. Folia opposita anguste elliptica acuminata basi obtusa 12–14 cm. longa 4.0–4.5 cm. lata subcoriacea indistincte venosa subtus glaucescentia; petiolo 5–7 mm. longo. Inflorescentia lateralis alternata laxa et ca. 10- vel 16-flora simplice cincinnata; pedunculo ca. 20 cm. longo gracillimo, internodio primario ca. 10 cm. longo; pedicellis ca. 2 cm. longis; bracteis trigonalibus ca. 1 mm. longis. Flores luteoli; calycis laciniis late trigonalibus ca. 1 mm. longis, squamellis oppositis subaequilongis irregulariter laceratis; corolla salverformi, tubo late cylindrico ca. 9 mm. longo medio ca. 2.5 mm. diam. extus glabro intus exappendiculato prope insertionem staminis piloso caeterumque glabro, ostio valde incrassato ibique rubro-tincto dicitur, lobis patulis ca. 1.5 cm. longis prope basim ca. 3 mm. latis deinde abrupte angusteque caudato-acuminatis et spiraliter contortis; antheris inclusis sessilibus anguste lanceolato-sagittatis basi anguste 2-lobatis ca. 5 mm. longis dorso glabro; carpellis anguste conico-oblongoides ca. 2 mm. longis glabris, nectariis 5 valde discretis compresse oblongoides ca. 1 mm. longis; stigmate oblongo-fusiformi basi indistincte annulato ca. 1.5 mm. longo.

COSTA RICA: PUNTARENAS: vicinity of Casacajal, Hacienda Sta. María 25 km. ESE of Puntarenas, alt. 30–100 m., July 3, 1949, *R. W. Holm & H. H. Iltis 243* (HOLOTYPE, MO).

This extremely distinct species comes as a great surprise, since its only close relative is *P. agglutinata* of Hispaniola and Puerto Rico. From the latter *P. caudata* is distinguished very sharply by the very long-pedicellate flowers with the peculiar corolla lobes longer than the tube.

ASCLEPIADACEAE

Matelea **rivularis** Woodson, spec. nov.

Suffrutices mediocres 2–4 dm. alti parce ramosi; ramis gracilibus ca. 1 mm. diam. juventate minute appresse pilosulis mox glabratis. Folia opposita; lamina lineari-elliptica acuminata 2–5 cm. longa 4–6 mm. lata basi in petiolum ca. 3–5 mm. longum gradatim angustata membranacea utrinque glabra subtus pallidiori. Inflorescentiae subterminales interpetiolares pedunculatae umbelliformes parviflorae; pedunculo 1–2 cm. longo minute appresse pilosulo; pedicellis tenuibus 1.5–2.0 cm. longis ut in pedunculo vestitis; bracteis minutis. Calycis laciniae ovato-deltoideae obtusae ca. 2 mm. longae extus dense pilosulae intus in marginibus 1-glandulosae. Corolla livide brunnea vel rubra rotata ca. 1.5 cm. diam.; lobis ovato-oblongis late acutis 7–8 mm. longis glabris; fauce parce annulato. Corona depresse pentagono-patelliformis ca. 1.5-diam. segmentis 5 majoribus leviter divisis margine humile arcuato intus inconspicue umbonatis cum 5 minoribus obtuse dentatis sequentibus alternatis. Gynostegium subsessile discoideum ca. 1.25 mm. diam. depresse umbonatum; pollinii corpusculo minute sagittato-lineari ca. 0.2 mm. longo, saccis late obovatis cum caudiculo hyalino inciso perbrevi ca. 0.3 mm. longis. Folliculi erecti pedunculo pedicelloque erectis fusiformes ca. 2.5–3.0 cm. longi saepe 1 cm. crassi laeves glabri; seminibus multis parvis rhomboideo-ovalibus suberoso-marginatis ca. 2 mm. longis.

Ecuador: santiago-zamora: near Méndez, alt. 1750–2500 ft., uplands along Río Upano just north of junction with R. Chupiantza, Nov. 14, 1944, *W. H. Camp E-1006* (holotype, MO); Cordillera Cutucú, ca. 20° 40′ S., 78° W., on rocks, subject to periodic overflow, covered twice in 10 days, and this the "dry" season, the water with terrific force, Nov. 17–Dec. 5, 1944, *Camp E-1211* (NY).

Peru: san martin: Cahazuta, Río Hualaga, alt. about 260 m., forest, March, 1935, *G. Klug 4036* (MO); Pongo de Cainarachi, Río Cainarachi, tributary of Río Hualaga, alt. about 230 m., forest, *Klug 2726* (MO); San Roque, alt. 1350–1500 m., Jan.–Feb., 1930, *Ll. Williams 7724* (MO); Tarapoto, alt. 750 m., December, 1929, *Williams 6010* (MO).

The Klug and the Williams specimens doubtless are distributed in many herbaria as "*Acomosperma rivularis* K. Sch.", under which they were received at the Missouri Botanical Garden. As nearly as I can ascertain, this name has been published only as a *nomen nudum* in E. Ule's account of the riparian vegetation of the Cainarachi river (Die Pflanzenformationen des Amazonas-Gebietes II. in Engl. Jahrb. 40:406. 1908). The plants must be rather common in the middle highland drainage of eastern Peru and Ecuador.

The species is a typical *Matelea* and strikingly parallel to the original element of the genus, *M. latifolia* Aubl. and *M. palustris* Aubl. of the Guianas.

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FLORA OF PANAMA

BY

ROBERT E. WOODSON, Jr.

AND

ROBERT W. SCHERY

AND COLLABORATORS

PART IV

Fascicle 2

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Vol. XLVII MAY, 1960 No. 2

FLORA OF PANAMA

Part IV. Fascicle 2*

CHLORANTHACEAE

By LORIN I. NEVLING, Jr.

1. HEDYOSMUM Sw.

Hedyosmum Sw. Prod. Fl. Ind. Occ. 84. 1788.

Tafalla Ruiz & Pav. Prod. 136. *t. 29.* 1794.

Dioecious or monoecious aromatic shrubs or small trees. Leaves opposite, generally elliptic to lanceolate, pinnately veined, margin serrate, the petioles connate into a pronounced petiolar sheath enclosing first the apical bud and later the stem, stipules setose to fimbriate. One or two superposed axillary buds may develop from each leaf axil, these buds sometimes becoming exserted from the petiolar sheath by elongation in the nodal region. When the inflorescence is monoecious the terminal bud and the first pair of subtending axillary branches often bear pistillate flowers, while the second and subsequent pairs bear staminate flowers. Staminate catkin of 1 to several cylindrical spikes which greatly elongate at anthesis; flowers naked, ebracteate, sessile or subsessile, each composed of a single bilocular stamen, the connective variously produced, the anthers longitudinally dehiscent. Pistillate inflorescence racemiform, paniculiform or spiciform; flowers monochlamydeous, bracteate, perianth fused into a tri-lobed urceolate cup persistent in fruit; ovary unilocular, uniovulate; style short, deciduous; fruit a small three-angled drupe.

Approximately 50 species. Mexico southward to Peru, Bolivia and Brazil; the Antilles; Asia.

a. Plants monoecious; pistillate flowers borne singly, the bracts free; leaves narrowly lanceolate to elliptic.......... 1. H. brenesii

aa. Plants dioecious; pistillate flowers borne singly or in groups of two or more, the bracts connate; leaves elliptic to broadly lanceolate.......... 2. H. calloso-serratum

1. Hedyosmum brenesii Standl. in Field Mus. Publ. Bot. 18:371. 1937.

Monoecious shrubs 1–2 m. tall, the branchlets terete, smooth to rugose. Leaves narrowly lanceolate to narrowly elliptic, 5–16 cm. long, 1–3 cm. broad, attenuate

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at the apex, cuneate-attenuate to rounded at the base, glabrous to minutely scabrous above and below, margin coarsely serrate except at the smooth base, the primary lateral veins obscure, the petiolar sheath 5–10 mm. long, the petiole 1–6 mm. long; stipules fimbriate or erose. Staminate catkin spiciform, about 5 mm. long, elongating slightly at anthesis, the primary peduncle generally unbranched; staminate flowers with the anthers about 1 mm. long, sessile, the connective apiculate, produced beyond the anthers 0.25 (–0.5) mm. Pistillate inflorescence often falsely dichotomous and then cincinnoid, the primary peduncle often white-spotted; pistillate flowers borne singly, sessile, the perianth urceolate, about 1.5–2.5 mm. long, 1.0–1.5 mm. in diameter, white; the stigma shortly exserted, the bracts free, ovate, to 2.5 mm. long, 1.5 mm. broad; fruit ovoid, 3.0–4.5 mm. long, 2.5–3.5 mm. in diameter, white.

Known only from Costa Rica and Panama.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Fish Creek Hills, *von Wedel 2362*.

Woodson and Schery have indicated previously (in Ann. Mo. Bot. Gard. 29:350. 1942) that this species might be synonymous with *Hedyosmum nutans* Sw. of the Greater Antilles. *Hedyosmum brenesii* differs from *H. nutans* primarily in inflorescence structure and in fruit size and color. In distinguishing between these two species I am indebted to C. E. Wood, Jr., for the use of his unpublished manuscript.

2. HEDYOSMUM CALLOSO-SERRATUM Oerst. in Vidensk. Meddel. Kjoeb. 1856:40. 1857.

Hedyosmum scaberrimum Standl. in Field Mus. Nat. Hist. 4:200–201. 1929.

Dioecious trees to 10 m. tall, the young branchlets generally rugose and somewhat scabrous. Leaves elliptic to broadly lanceolate, 9–18 cm. long, 3–7 cm. broad, narrowly acute to abruptly acuminate at the apex, broadly cuneate to cuneate-attenuate at the base, scabrous above and below, margin serrate but sometimes entire towards the base, the costa and primary lateral veins sometimes with small irregular enations, the petiolar sheath smooth or serrulate-winged, 1.25–2.5 cm. long, the petiole 0.5–2.5 cm. long; stipules setose or fimbriate. Staminate shoot apex and several subtending nodes usually flowering at one time, the inflorescence compound, composed of a terminal spike and generally several lateral spikes, each floriferous peduncle subtended by a lanceolate to elliptic bract, the spikes 3–5 cm. long at anthesis; staminate flowers with the anther 2.0–2.5 mm. long, sessile, the connective apiculate, produced beyond the anther about 0.25 mm. Pistillate inflorescence paniculiform; pistillate flowers borne singly or in groups of 2–5, the perianth urceolate, 2.5–3.0 mm. long, 1.5–1.75 mm. in diameter, white, pedunculate, the stigma and style clavate, about 1 mm. long, exserted, deciduous, the bracts connate, callose at the apex.

Nicaragua, Costa Rica and Panama.

BOCAS DEL TORO: region of Almirante, Buena Vista Camp on Chiriquí Trail, *Cooper 595*; vicinity of Chiriquí Lagoon, Bastimentos "short cut", *von Wedel 2901*; vicinity of Chiriquí Lagoon, Old Bank Island, *von Wedel 1943*. CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, *P. White 28*. COCLÉ: hills north of El Valle, *Allen 2284, 2418*.

Whether *Hedyosmum scaberrimum* and *H. calloso-serratum* should be treated as separate species or a single species is difficult to determine. In Panama it almost appears as though two distinct species are present. The specimens generally can be separated on the basis of whether or not the fruiting branches are enclosed at the base by the petiolar sheath; the relative length of the petiolar sheath in respect to lamina length; presence or absence of serrulate-winging of the petiolar sheath; setose *vs.* fimbriate stipules. However, examination of specimens from Costa Rica and Nicaragua indicates that these characters or combinations thereof intergrade so thoroughly that separation is no longer possible. For this reason I prefer to treat the group as a single species.

Fig. 24. *Hedyosmum brenesii*

LACISTEMACEAE

By LORIN I. NEVLING, Jr.

Shrubs or trees. Leaves alternate, distichous, simple, pinnately veined, petiolate; stipules caducous. Inflorescences generally fasciculate, axillary, spicate, racemiform or paniculiform; bracteate. Flowers bisexual or unisexual, when unisexual the plants polygamo-andromonoecious, small, 2-bracteolate; naked or monochlamydeous with 6 or fewer perianth segments connate at the base or free, equal or unequal; annular hypogynous disc present; stamen 1, inflexed, longitudinally dehiscent; ovary superior, 3-carpellate, 1-locular, the placentation parietal, the ovules 3–6, anatropous, pendulous, the stigma trifid; fruit a capsule dehiscing by 3 valves; seeds 1–3, testa sometimes fleshy.

Two genera, both represented in Panama.

a. Inflorescences many-fascicled, spiciform or racemiform; plants bisexual; bracteoles free; pedicel at most ¼ as long as the flower; perianth lobes present or absent, free, often erose, often unequal; anther connective bifurcate distally........ 1. Lacistema

aa. Inflorescences solitary to few-fascicled, racemiform or paniculiform; plants bisexual (in Panama) or polygamo-andromonoecious; bracteoles connate; pedicel at least as long as the flower; perianth lobes present, connate at the base, not erose, equal; anther connective not bifurcate distally........ 2. Lozania

1. LACISTEMA Sw.

Lacistema Sw. Prod. Veg. Ind. Occ. 12. 1788.

Nematospermum A. Rich. in Act. Soc. Hist. Nat. Par. 1:105. 1792.
Synzyganthera Ruiz & Pav. Prod. Fl. Per. & Chil. 137, *t. 30.* 1794.
Didymandra Willd. Sp. Pl. 4:971. 1805.

Shrubs or small trees, the young branches glabrous or rarely pubescent. Leaves membranaceous to coriaceous, margin sometimes distantly serrate; stipule scars sometimes almost encircling the young stem. Inflorescences spicate or rarely racemiform, as many as 35 spikes per axil, generally equal to or exceeding the petiole of the subtending leaf. Flowers bisexual; bracteoles free; perianth present or absent, free, often erose, often unequal, white or cream; anther connective bifurcate distally. Fruit a red globose or subglobose capsule, sessile or on a short gynophore; seeds white.

About 35 species in tropical America. Only 1 species represented in Panama.

1. Lacistema aggregatum (Berg) Rusby, in Bull. N. Y. Bot. Gard. 4:447 1907.

Piper aggregatum Berg, in Act. Helv. 7:131, *t. 10.* 1772.
Lacistema myricoides Sw. Prod. Veg. Ind. Occ. 12. 1788.
Piper fasciculare Rudge, Pl. Guian. *t. 4.* 1805.
Lacistema oblongum Spreng. Syst. 1:124. 1825.
Lacistema elongatum Schnizl. in Mart. Fl. Bras. 4^1:282. 1857.
Lacistema myricoides var. *β stipitatum* DC. in DC. Prod. 16^2:592. 1868.

Fig. 25. *Lacistema aggregatum*

Shrubs or trees to 18 m., the young branches glabrous or strigose. Leaves lanceolate to obovate-lanceolate, 7–17 cm. long, 2.0–7.5 cm. wide, apex attenuate, cuneate to rounded at the base, membranaceous to subcoriaceous, generally glabrous above, glabrous or sparsely strigose below, the margin entire to distantly and broadly serrate; petiole 5–7 mm. long; stipules 5–9 mm. long. Inflorescence of cylindrical spikes, 4–12 per axil; bracts broader than long, one subtending each flower. Flowers sessile, monochlamydeous; bracteoles at most 1 mm. long; perianth segments 4, about 0.5 mm. long, erose, unequal; disc about 0.75 mm. long, fleshy; stamen almost 1 mm. long, glabrous; stigma exserted; fruit 6–8 mm. long, about 6 mm. in diameter, often on a gynophore to 3 mm. long.

Mexico to Peru, Bolivia, Brazil; Antilles and the West Indies.

BOCAS DEL TORO: Old Bank Island, *von Wedel 1964*. CANAL ZONE: woods along Pavon Road, *Johnston 1777*; Gatún, *Hayes s. n.*; swamp south of mouth of Río Chagres, *Johnston 1697*; Chagres, *Fendler 282, Grisebach s. n.* COCLÉ: hills south of El Valle de Antón, alt. about 700 m., *Allen 2476*. PANAMÁ: Cerro Campana, trail from Campana to Chica, alt 600–800 m., *Allen 2646*.

2. LOZANIA Mutis

Lozania Mutis, in Contin. Seman. Nouv. Reino de Granada, 3:20. 1810.

Monandrodendron Mansf. in Notizbl. 10:861. 1929.

Shrubs or trees, the young branches pubescent or rarely glabrous. Leaves generally pubescent below, membranaceous to subcoriaceous, the margin entire or serrate; stipule scars at most half encircling the young stem. Inflorescences racemiform or paniculiform, solitary or as many as 5 per axil, always much longer than the petiole of the subtending leaf. Flowers bisexual or unisexual, bracteoles connate, the perianth monochlamydeous, connate at the base, equal, white to yellow-green. Fruit a small globose capsule, sessile.

Six species, Central and South America.

a. Racemes solitary; leaves broadly obovate-elliptic; bracts densely pubescent; staminal filament much longer than broad.. 1. L. PEDICELLATA
aa. Racemes solitary or 2–3; leaves elliptic to oblong-elliptic; bracts glabrous; staminal filament as long as broad.. 2. L. MONTANA

1. Lozania pedicellata (Standl.) L. B. Smith, in Phytologia 1:138. 1927.

Lacistema pedicellatum Standl. in Journ. Wash. Acad. Sci. 17:8. 1927.

Shrubs or trees to 7.5 m. tall, the young branches strigose. Leaves broadly obovate-elliptic, 8–12 cm. long, 2.5–4.5 cm. broad, obtusely or acutely acuminate, broadly cuneate, membranaceous, glabrous above, the costa, lateral veins and vein axils strigose below, the margin minutely serrate; petiole 3–8 mm. long; stipules 1.5–2.0 mm. long. Inflorescence racemiform, solitary, to 9 cm. long; bracts densely pubescent, about 0.75 mm. long, 0.5 mm. broad. Flowers bisexual; bracteoles about 0.5 mm. long; pedicel 0.75–2.0 mm. long, the perianth lobes broadly rounded, about 0.5 mm. long; disc fleshy; stamen about 0.5 mm. long, exserted, the filament much longer than broad, the anther cells small; ovary globose, about 0.5 mm. long, pubescent, the stigma subsessile; fruit about 4 mm. in diameter, sparsely puberulent, seeds 3.

Panama.

BOCAS DEL TORO: region of Almirante, *Cooper 568*; Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 2121*. CANAL ZONE: Barro Colorado Island, Gross Pt., *Aviles 972*. COLÓN: along the Río Culebra, above Santa Isabel, near sea level, *Pittier 4152*.

2. Lozania montana Standl. in Field Mus. Pub. Bot. 18:722. 1937.

Trees to 40 m. tall, the young branches sparsely strigose. Leaves elliptic to oblong-elliptic, 6–12 cm. long, 1.5–3.5 cm. broad, apex obtusely attenuate-acuminate, base broadly cuneate, subcoriaceous, glabrous above, the costa, lateral veins and vein axils sparsely strigose below, the margin serrate; petiole 9–12 mm. long; stipules about 2 mm. long. Inflorescences racemiform, rarely solitary generally 2 or 3, to 6 cm. long; bracts glabrous, 0.75–1.25 mm. long, 0.5–1.0 mm. broad. Flowers bisexual; bracteoles about 1 mm. long; pedicel 1.5–3.0 mm. long, the perianth lobes broadly rounded, to 1.25 mm. long; disc fleshy; stamen about 0.5 mm. long, exserted, the filament as long as broad, the anther cells small; ovary

globose, about 0.5 mm. long, pubescent, the stigma subsessile; fruit about 3.5 mm. long, 3 mm. in diameter, glabrous or sparsely puberulent.

Costa Rica and Panama.

CHIRIQUÍ: Bajo Mono–Robalo Trail, alt. 5000–7000 ft., western slope of Cerro Horqueta, *Allen 4842*.

SALICACEAE

Salicaceae, including the poplars *(Populus)* and willows *(Salix)*, have not yet been encountered in Panama. *Salix chilensis,* however, is an occasional escape from cultivation in Costa Rica and is to be expected in Chiriquí.

Fig. 26. *Lozania pedicellata*

MYRICACEAE

By LORIN I. NEVLING, Jr.

1. MYRICA L.

Myrica L. Sp. Pl. 1024. 1753.

Gale Tourn. ex Adans. Fam. 2:345. 1763.
Nageia Gaertn. Fruct. 1:191. 1788.
Morella Lour. Fl. Cochinch. 548. 1790.
Cerophora Raf. Alsog. Am. 11. 1838.
Fayana Raf. loc. cit. 12. 1838.
Pimecaria Raf. loc. cit. 64. 1838.
Faya Webb & Berth. Hist. Nat. Canar. Bot. 2^3:272, *t. 216*. 1850.

Monoecious or dioecious shrubs or small trees. Leaves simple, alternate, often glandular below, generally fragrant; estipulate. Inflorescence spicate, axillary. Flowers small, achlamydeous, bracteate, sometimes also bracteolate. Staminate flowers with 2–30 stamens, the filaments free or connate, the anthers longitudinally dehiscent. Pistillate flowers 2-carpellate, the ovary 1-locular, the ovule 1, orthotropous, the stigmas 2, filiform. Fruit a small drupe with a wax-secreting exocarp, often warty; embryo straight, surrounded by a 1-layered oily endosperm, the cotyledons thick, plano-convex.

Only one species represented in Panama.

1. Myrica mexicana Humb. & Bonpl. ex Willd. Enum. Hort. Berol. 2:1011. 1809.

Myrica xalapensis Kunth, in HBK Nov. Gen. 2:16. 1817.

Dioecious trees to 8 m. tall, the branches punctate-glandular, hirsute. Leaves oblanceolate, 3.5–12.0 cm. long, 1–3 cm. wide, generally smaller in pistillate plants than in staminate plants, apex acute, attenuate at the base, subcoriaceous, both surfaces glandular-punctate, margin entire to distantly dentate, aromatic; petioles 1–3 mm. long. Flowers subtended by a pair of linear bracteoles and an ovate bract, the bracteoles about 0.75 mm. long, deciduous, the bract about 1.0–1.5 mm. long, 0.75 mm. broad, glandular-punctate on abaxial surface only, margin minutely ciliate at least towards the apex. Staminate flowers (described from Mexican specimens) with 4 (–5) stamens, the filaments about 1.5 mm. long, basally connate. Pistillate flowers with globose ovary about 0.5 mm. tall, 0.5 mm. in diameter, glandular-punctate, strigose apically, the stigmas about 2 mm. long; fruit ovoid, to 4 mm. long, 3 mm. in diameter, warty.

Mexico to Panama. In Panama found along margins of residual patches of forest in dry windswept grasslands.

PANAMÁ: Cerro Campana, *Allen 2084*; Cerro Campana, trail from Campana to Chica, alt. 600–800 m., *Allen 2654*.

Fig. 27. *Myrica mexicana*

JUGLANDACEAE

By WAYNE E. MANNING

Trees or rarely shrubs; buds naked or scaly, often several superposed; leaves usually deciduous, alternate, rarely opposite or whorled, estipulate, pinnately compound; leaflets entire or serrate, glandular-dotted beneath; flowers monoecious or rarely dioecious, staminate or pistillate flowers or both in elongate drooping or erect catkins or spikes; staminate and pistillate inflorescences sometimes separate, sometimes combined into an androgynous panicle with central spike wholly or partly pistillate and the lateral branches staminate; separate staminate inflorescence a cluster of 3–8 catkins or a solitary catkin; separate pistillate inflorescence a catkin, a few-flowered spike, or a solitary flower; inflorescences terminal, or lateral on old wood, or the staminate sometimes lateral at the base of the new growth; staminate calyx commonly 4-lobed, or lacking, the subtending entire or 3-lobed bract and 2 bracteoles usually appearing as part of the perianth; petals none; stamens 3–many; pistillate calyx usually 4-lobed, or absent, the subtending 3-lobed or entire bract and 2 or 3 bracteoles fused only with the pedicel and base of the ovary or with the whole ovary, a ring of minute inner bracteoles very rarely present; ovary inferior, 1-celled above, 2- to 4- to 8-celled below, with one erect orthotropous ovule in the center at the top of the primary partial partition; style one, with usually 2 stigmatic branches; fruit a nut enclosed in a husk, or a nut with a thin dry skin, or a nutlet with 2 or 3 wings; seed solitary, large 2–4–8-lobed, without endosperm; cotyledons 4-lobed, oily, at germination remaining in the nut or appearing above ground.

1. ALFAROA Standl.

Alfaroa Standley in Journ. Wash. Acad. Sci. 17:78. 1927; Manning, in Bull. Torr. Bot. Club, 76:196–209. 1949; Standley, in Flora of Costa Rica, Field Mus. Publ. Bot. 18:372–374. 1937. Manning, in Standley and Steyermark, Flora of Guatemala, in Fieldiana: Botany, 24: Part III, 353–354. 1952.

Trees or large shrubs; leaves opposite or whorled, pinnately compound, without a terminal leaflet, the leaflets several to many, alternate or frequently opposite, serrate or entire, lepidote beneath at least on the youngest leaves; pith of branchlets solid; flowers monoecious or partially dioecious, the inflorescence terminal, consisting usually of an androgynous open or spike-like panicle, the main portion pistillate, with 30–50 flowers, bearing near the base usually 2–4 lateral short or elongate branches, these staminate, the staminate catkins sometimes forming a separate terminal panicle on different branches or on different trees; bracts of the staminate flowers minute, 3-lobed, beneath the calyx, the 2 bracteoles and 2–4 variable sepals together appearing as an irregular 4–6 lobed calyx, the lobes oblong, obtuse; stamens 6–12, inserted in a single series around a naked center or rarely around a rudimentary ovary, the filaments almost obsolete; anthers 2-celled, glabrous,

Fig. 28. *Alfaroa costaricensis*

dehiscent by longitudinal slits; pistillate flowers sessile, subtended by a minute 3-lobed bract shorter than the ovary; perianth deeply 4-lobed, the lobes oblong-linear, unequal, obtuse, erect, persistent upon the apex of the fruit; style shorter than the perianth lobes, bifurcate, the stigmas subglobose; fruit oval or obovoid, small, 2–3 cm. long, the skin ("pericarp" or "exocarp") almost dry, thin, indehiscent, adhering closely to the nut proper ("endocarp"); nut thin-walled, loculicidally dehiscent at time of germination of the seed, falsely 8-celled in the lower half, 4-celled above the middle, 1-celled at the very apex, the partitions nearly complete, with lamellae projecting from them into the loculus; seed 8-lobed to the base, each cotyledon 4-lobed.

1. Alfaroa costaricensis Standl. in Jour. Wash. Acad. Sci. 17:78. 1927.

A large shrub or a tree, the bark almost smooth, pale brownish; branchlets and leaf rachises usually densely hirsute with long stiff spreading hairs, sometimes merely hirtellous or in age glabrate; leaves almost all opposite, those of a pair often unequal, or one of the leaves sometimes suppressed; petiole 1–2 (–3) cm. long; leaflets mostly 10–20, highly variable, often almost all opposite, oblong to narrowly lance-oblong, mostly 10–18 cm. long and 1.5–4 cm. wide, the lowest leaflets generally much reduced, acute to long-acuminate or rarely obtuse, sessile or nearly so, obtuse to truncate at the base and usually very oblique, conspicuously appressed-serrate or almost entire, membranaceous or thicker, glabrous or nearly so along the costa, usually glaucous or glaucescent beneath, usually hirtellous or hirsute along the nerves but sometimes glabrate, inconspicuously lepidote; flower spikes stout, 3–5 cm. long, short-pedunculate, the rachis densely hirtellous and glandular; staminate flowers 4 mm. broad, the perianth glandular; pistillate flowers green, 5–6 mm. long; ovary sparsely hirtellous and densely covered with golden glands; stigmas red; fruiting spikes 12–18 cm. long or more, each bearing numerous oval or obovoid fruits, about 2.5 cm. long and 2 cm. thick, densely velutinous-hirsute and covered with sessile glands; nut not ridged, broadly rounded at base and apex, the wall ("endocarp") less than 1 mm. thick.

Mountains of Guatemala, Costa Rica, and Panama.

CHIRIQUÍ: Boquete region, Cerro Horqueta-cloud forest, 6500 ft., *Von Hagen & Von Hagen 2096, 2179*.

These specimens are from young, non-fruiting trees, with the twigs and rachises strongly hairy.

Alfaroa manningii Leon, described by Jorge Leon from Costa Rica in Ceiba 42:46, 1953, and recently collected in Colombia, undoubtedly occurs in Panama. In this species the leaf has 8–12 leaflets, strongly lepidote beneath, the lower leaflets not much reduced, the petiole is 4–7 cm. long, and the fruit is glabrous, ridged.

Engelhardtia and *Juglans* may occur in Panama. The former occurs in Mexico, Guatemala, and Costa Rica. *Juglans* occurs in U. S., Mexico, Honduras, Guatemala, in seven South American countries, and in the West Indies.

CORYLACEAE

By LORIN I. NEVLING, Jr.

Monoecious trees or shrubs. Leaves alternate, simple, serrately margined, petiolate; stipulate. Inflorescences unisexual, compound, composed of spirally arranged, condensed and sometimes reduced cymules, catkin-like, bracteate, the staminate pendent, the pistillate pendent or erect. Staminate inflorescence composed of 3-flowered cymules (reduced in distal portion of catkin); primary bract 1, secondary bracts 0 or 2, tertiary bracts 0, 2, (3 or 4); perianth present or absent, tepaloid; stamens 2–20 per cymule, the filaments short, free or basally connate, generally adnate in part with the tepals, the anthers 2-celled, cells separate or connate, dehiscing longitudinally. Pistillate inflorescence composed of 2- or 3-flowered cymules; primary bract 1, secondary bracts 0 or 2, tertiary bracts 0, 2, or 4; perianth present or absent, generally tepaloid though sometimes reduced to small glands; pistil 1, the ovary 2- or 3-carpellate, inferior or nude, 2- or 3-locular below, 1-locular above, each locule functionally 1-ovulate, the placentation basically axile, the ovules with 1 integument, the styles 2; fruit a small nut or samara, indehiscent, the embryo straight, exendospermous, cotyledons oil-bearing.

Six genera, approximately 100 species. Represented in Panama by a single genus.

1. ALNUS Gaertn.

ALNUS Gaertn. Fruct. & Sem. 2:54. 1791.

Alnaster Spach, in Ann. Sc. Nat. Ser. II. 15:200. 1841.
Clethropsis Spach, loc. cit. 201. 1841.
Semidopsis Zumaglini, Fl. Pedem. 1:249. 1849.
Duschekia Opiz, Seznam. 38. 1852.
Alnobetula Schur, in Verh. Siebenb. Ver. Naturw. 4:68. 1858.

Terminal buds present; stipules caducous. Staminate catkins borne at the end of last year's leaf shoot; cymules 3-flowered (often reduced at distal portion of catkin), subtended by a primary bract, 2 secondary bracts and each lateral flower by a single abaxial bract (rarely an adaxial bract develops); tepals 0–6; stamens 4(–6), adnate to the tepals. Pistillate catkins borne on few-leaved dwarf-shoots or borne in a leaf axil subtending the staminate catkin, often several lateral catkins develop to form a raceme, each cymule composed of 2 lateral flowers, the bracts as in staminate cymules; perianth reduced to small glands which are sometimes adnate to the ovary; the catkin at maturity resembling a small cone; ovary 2- or 3-carpellate. Fruit a nut more or less winged. The presence of polymerous flowers in the same cymule is not unusual. Hermaphroditic flowers are sometimes found toward the base of the catkin (either staminate or pistillate).

Species approximately 20, only 1 in Panama.

1. Alnus ferruginea HBK. Nov. Gen. & Sp. 2:17. 1817.

Alnus acuminata var. *ferruginea* (HBK) Regel, in Mém. Soc. Nat. Moscow 8:148. 1861.
Alnus jorullensis var. γ *ferruginea* (HBK) O. Ktze. Rev. Gen. 3[2]:295. 1898.

Trees to 25 m. tall, the branches terete, more or less glabrous, the buds sparsely ferrugineous-velutinous. Leaves ovate to ovate-lanceolate, 5–17 cm. long, 3–7 cm. broad, acute to acuminate at the apex, obtuse to rounded at the base, margin serrate, peltate glandular above when young, peltate glandular and ferrugineous-velutinous below; petiole 0.6–1.7 cm. long, densely velutinous to almost glabrous. Staminate catkin (immature) to 2.5 cm. long, about 4 mm. in diameter, shortly stalked to subsessile. Staminate flowers small; tepals 4, more or less oblong, incised, to 1.25 mm. long, 0.5 mm. broad; stamens 4, opposite the tepals, the filaments short, adnate at their bases to the tepals, the anthers oblong, to 1 mm. long, 0.5 mm. broad. Pistillate catkin at maturity an ovoid cone, 1–2 cm. long, 0.7–1.2 cm. in diameter. Pistillate flowers small; pistil less than 0.5 mm. long, the styles 2, spreading; fruit samaroid, obcordate, 2.5–3.5 mm. long, 1.5–2.5 mm. broad.

A common tree in the Chiriquí Volcano region where it forms almost pure stands or sometimes intermixes with oaks. Occupies about 20% of the forest stand in the 8,000–10,000 ft. zone.

The status of this group is not definite. It has been assigned specific rank and also varietal rank in two species. The most practical position is to retain it as a species until further evidence indicates a change of status to be necessary.

CHIRIQUÍ: Finca Lérida to Peña Blanca, alt. 1750–2000 m., *Woodson & Schery 317*; valley of the upper Río Chiriquí Viejo, *White & White 57*, *P. White 319*; Volcán de Chiriquí, *Davidson 997*; Llano del Volcán, alt. 1500–1600 m., *Allen & Fairchild 3468*; Bajo Chorro, Boquete District, *Davidson 173*; summit and SW face of Cerro Copete, alt., 9000 ft., *Allen 4895*.

Fig. 29. *Alnus ferruginea*

FAGACEAE

BY C. H. MULLER

1. QUERCUS L.

QUERCUS L. Gen. Pl. ed. 5. 431. 1754.

Erythrobalanus Schwarz, Notizbl. Bot. Gart. Mus. Berlin-Dahlem 13:8. 1936.
Macrobalanus Schwarz, Notizbl. Bot. Gart. Mus. Berlin-Dahlem 13:8. 1936.

Trees or shrubs; leaves alternate, simple, petiolate, blades entire, toothed, or lobed, persistent or deciduous, stipules associated with the buds, ligulate, often caducous; flowers monoecious; staminate flowers in flaccid pendulous aments, the perianth about 5-lobed, stamens 5 to 10, free; pistillate flowers solitary or clustered, subsessile or peduncled, enclosed in an involucre of numerous flat scales, the perianth 6-lobed, ovary 3-carpellate, 1-celled, ovules 6 (5 abortive), styles 3, short; fruit a nut (acorn), 1-seeded, partly enveloped by an involucre (cup) of flat or basally thickened scales, maturing in 1 or 2 seasons.

The oaks comprise a more or less temperate zone group and are therefore, with few exceptions, confined in Panama to the high mountains near the Costa Rican boundary, apparently no species occurring below an elevation of 1200 m. In addition to the ten species definitely known to exist in Panama, it is very likely that several of the closely adjacent Costa Rican species may also occur across the boundary in the higher mountains of upper Panama. Future more detailed collections in this area will possibly reveal these as well as a few additional undiscovered endemics.

a. Bark rather soft gray and scaly, leaves if toothed only mucronately tipped or rounded, never spinose- or aristate-tipped, stigmas abruptly dilated on short styles, fruit annual, cup scales usually prominently thickened basally and loosely appressed apically, acorns with the shell glabrous on the inner surface, abortive ovules basal..........subgenus LEPIDOBALANUS. White oaks.
  b. Twigs of the season persistently and densely fulvous-tomentose.
    c. Leaves obovate to elliptic-oblanceolate, not tapering, the base rather broad, cuneate to cordate, subentire or low-toothed, petioles over 6 (usually over 10) mm. long.
      d. Leaves deeply broad-cordate.......... 1. Q. SEIBERTII
      dd. Leaves cuneate to truncate at base.......... 2. Q. DAVIDSONIAE
    cc. Leaves oblanceolate, tapering to a cuneate or narrowly rounded base, coarsely toothed above the middle, petioles 3 to 5 mm. long. 3. Q. OOCARPA
  bb. Twigs of the season glabrate or sparingly pubescent or gray-tomentose.
    e. Leaves completely glabrate.
      f. Leaves long-acuminate, entire, fruit very small, cup scales tomentose at base only, the apices glabrous, thin, and loosely appressed.......... 5. Q. PANAMANDINAEA
      ff. Leaves not acuminate, or if so then coarsely toothed, fruit very large, cup scales pubescent all over.......... 4. Q. CORRUGATA
    ee. Leaves villous or tomentose beneath or at least the midrib strigose or stellate-tomentose.
      f. Leaves rarely over 6 (8) cm. long, acorns scarcely more than 1 cm. in diameter.......... 6. Q. COPEYENSIS
      ff. Leaves rarely less than 10 cm. long, acorns 2.5 cm. broad or broader.
        g. Leaves obovate to elliptic-oblanceolate, not markedly tapering, the base rather broad, cuneate to cordate, obscurely low-toothed, petioles 6 to usually 10 or 12 mm. long.......... 2. Q. DAVIDSONIAE

gg. Leaves oblanceolate, tapering to the cuneate or narrowly rounded base, coarsely toothed above the middle, petioles 3 to 5 mm. long .... 3. Q. OOCARPA

aa. Bark rather hard, black and furrowed but scarcely scaly, leaves if toothed aristate-tipped, never round-lobed or mucronate, stigmas gradually (or rather abruptly) dilated, on long styles, fruit biennial or annual, cup scales scarcely thickened basally (in Panama) and usually tightly appressed apically, acorns with the shell tomentose on the inner surface, abortive ovules apical or basal .... subgenus ERYTHROBALANUS. Black oaks

h. Cup scales very loosely appressed .... 7. Q. HUMBOLDTII

hh. Cup scales rather closely appressed.

i. Leaves small, averaging under 8 cm. long, glabrate except for discrete tufts in the axils of the principal veins beneath .... 8. Q. SEEMANNII

ii. Leaves large, averaging over 12 cm. long, distinctly pubescent about the midrib beneath

j. Petioles very short, 2–6 mm. long, blades very thin .... 9. Q. GULIELMI-TRELEASEI

jj. Petioles elongate, 12–23 mm. long, blades thick and coriaceous ... 10. Q. BARUENSIS

1. QUERCUS SEIBERTII C. H. Mull., U.S.D.A. Misc. Pub. 477:19. *pls. 6* & *7.* 1942.

Large tree to 25 m. tall. Twigs very coarse (4 to 7 mm.), markedly fluted, densely fulvous-tomentose, glabrate and gray the second year with conspicuous white lenticels. Buds glabrate, for a time surrounded by ligulate stipulelike scales; the stipules persistent for a time, 10 to 12 mm. long, ligulate, dorsally appressed-pubescent. Leaves deciduous, thin but firm, large (12 to 20 cm. long, 5 to 11 cm. broad), elliptic or broader above the middle, apically acute or broadly rounded, broadly and markedly cordate, entire, margins minutely revolute, upper surface somewhat shining, glabrous or glabrate from sparsely stellate-puberulent, midrib densely and conspicuously fulvous-tomentose, lower surface dull, minutely stellate-puberulent, the veins and midrib villous; veins about 13 to 15 on each side, much branched and obviously anastomosing near the margin, scarcely raised or even impressed above and very prominent (even to the reticulum) beneath; petioles 12 to 18 mm. long, 1.5 to 3 mm. thick, densely fulvous-tomentose. Pistillate catkins 3 to 9 cm. long, 3 to 6 flowers scattered on the pubescent peduncle, all except the basal 1 or 2 flowers aborting. Fruit annual, large; cups 3 to 4 cm. in diameter, openly shallow-goblet-shaped, the scales elongate-oblong, somewhat spreading or loosely appressed, finely pubescent, the lower ones dorsally thickened. Mature acorns unknown.

Quercus seibertii is most closely related to *Q. insignis* Mart. & Gal. of Mexico from which its long peduncles and entire cordate leaves with fewer veins amply distinguish it. These characters distinguish it equally well from *Q. davidsoniae*, to which it is less closely related. The species is known only from Panama.

CHIRIQUÍ: Upper valley of Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 225* (type), *Allen 1596*.

2. QUERCUS DAVIDSONIAE Standl., Field Mus. Bot. Ser. 22:14. 1940.

"Very tall" tree or reaching only 8 m. Twigs moderately coarse (2 to 5 mm. thick), fluted, from sparsely fulvous-tomentose glabrate and gray or brown with evident light lenticels. Buds round, glabrate; stipules caducous, about 10 mm.

Fig. 30. Panamanian species of *Quercus*

long, ligulate, dorsally tomentose. Leaves deciduous (?), thin but firm, 9 to usually 15 cm. long, 4 to 8 cm. broad, oblanceolate-oblong to oblong-elliptic, attenuately acute or merely acute at apex, cuneate or rounded or truncate at base, scarcely cordate, mucronately or rarely crenately toothed especially above, the teeth coincident with the veins, margins minutely revolute, upper surface somewhat shining, from very sparsely puberulent glabrate, lower surface somewhat shining, from puberulent glabrate or the veins pubescent; veins about 13 to 18 on each side, much branched and obviously anastomosing but ultimately passing into the teeth where those are present, scarcely raised above but quite prominent (including the reticulum) beneath; petioles 6 to 12 mm. long, about 1.5 mm. thick, from puberulent or tomentose becoming glabrous. Catkins? Fruit annual, solitary on a peduncle about 1.5 cm. long; cups 3.5 cm. broad, hemispheric, scales deltoid-ovate to oblong, attenuately narrowed but finally obtuse, thickened basally, loosely appressed, densely sericeous-tomentose; acorns (immature) subglobose, about 2.5 cm. long and 3 cm. broad, from buff-sericeous becoming glabrate.

Quercus davidsoniae is a polymorphic species, and it is therefore sometimes difficult to distinguish. Its specific relationship is not clear, but its toothed leaves and glabrescent twigs readily distinguish it from similar species. The species occurs also in Costa Rica.

CHIRIQUÍ: Distr. de Boquete, Boquete, *Davidson 864* (type).

3. QUERCUS OOCARPA Liebm., Overs. Danske Vidensk. Selsk. Forhandl. 1854:184. 1854.

Small or large tree (6 to 25 m.). Twigs rather coarse (3 to 5 mm.), fluted, from densely fulvous-tomentose becoming glabrate and gray or light brown with a few scarcely evident lenticels. Buds oblong, acute, about 4 mm. long, glabrous, with ligulate villous stipules 10 to 13 mm. long and persistent. Leaves apparently evergreen, thin and papery or rather firm, 10 to 25 or rarely 30 cm. long, 3 to 10 or even 14 cm. broad, oblanceolate to obovate or narrowly elliptic, attenuately acute at apex, narrowly rounded or cuneate at base, undulately or sharply low-dentate except the entire base, margins very minutely somewhat revolute, upper surface somewhat shining, glabrous or usually glabrescent from minutely puberulent, the midrib often persistently fulvous-tomentose, lower surface dull, persistently and sparsely villous especially on the veins and reticulum; veins about 14 to 22 on each side, much branched and obviously anastomosing near the margin but eventually passing into the teeth where those are present, slightly impressed above and very prominent (including the reticulum) beneath; petioles very short (3 to 5 mm. long), densely or sparsely fulvous-tomentose. Catkins? Fruit annual, rather large, solitary or paired on a peduncle 5 to 18 mm. long and 5 to 7 mm. thick; cups 3 to 4 cm. broad, openly goblet-shaped or cup-shaped, the scales triangular-ovate to oblong and narrowly obtuse, densely short-pubescent, loosely appressed; acorns depressed-subglobose or elliptic, 2.5 cm. long and 3 cm. broad or (in Panama material) 4 cm. long and 2.5 cm. broad, one-half or only one-fourth included.

Quercus oocarpa is not closely related to any other species in Panama. It is characterized by its large fruit and by its oblanceolate, toothed, attenuately acute leaves with markedly short and inconspicuous petioles. The species ranges north to Mexico.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 317*; Distr. de Boquete, Bajo Mono, *Davidson 497*; Boquete to Finca Lérida, *Allen 303*; Finca Lérida to Peña Blanca, *Woodson* and *Schery 286*.

4. QUERCUS CORRUGATA Hook., Icones Plant. 5: *pl. 403, 404.* 1842.

Small or large tree, 6 to 20 m. tall. Twigs slender or coarse (often on the same branch), 1.5 to 5 mm. thick, fluted, glabrous or from sparingly strigose soon glabrescent, brown but soon becoming gray with rather large pale lenticels. Buds about 3 mm. long, round-ovoid, glabrous, grayish brown, the stipules caducous, about 10 mm. long, ligulate, dorsally pubescent. Leaves deciduous, thick and rather hard, 5 to usually 15 or even 25 cm. long, 2 to 5 or even 7 cm. broad, lanceolate to oblanceolate or a broader form elliptic to obovate, acute to attenuately acuminate and the ultimate apex narrowly rounded or acute, basally cuneate to rounded, coarsely toothed with the teeth abruptly directed forward and mucronate-tipped, entire toward the base, margins minutely revolute or flat, both surfaces somewhat shining, glabrous, old leaves somewhat bullate-granular above or smooth; veins 12 to 14 or even 18 on each side, branching and more or less obviously anastomosing but ultimately passing into the teeth where those are present, minutely raised (including the reticulum) above, more prominent beneath; petioles 15 to 40 mm. long or rarely shorter, glabrous or puberulent. Staminate catkins 5 to 6 cm. long, sparsely villous, loosely flowered, the anthers much exserted. Pistillate catkins about 5 mm. long, 1- or 2-flowered. Fruit annual, solitary on a peduncle 5 to 10 mm. long, rather large; cups 3 to 4 or even 6 cm. broad, shallowly cup-shaped or hemispheric (or discoid in some Mexican forms), very thick, the scales broadly ovate with narrowed apices, much thickened basally, appressed, closely tomentose; acorns subglobose or ovate to oblong, 3 to 5 cm. in diameter, typically longitudinally corrugated but often smooth, dark brown, from sparsely villous glabrate, about one-half included.

Quercus corrugata is readily distinguished from all other species of LEPIDOBALANUS in our range by its usually narrow leaves with quite glabrate blades and its very large fruit. The species ranges from Mexico to Costa Rica and is very sparse in Panama.

CHIRIQUÍ: north of El Hato, Volcán Baru, *Stern* and *Chambers 47*.

5. QUERCUS PANAMANDINAEA C. H. Mull., U.S.D.A. Misc. Pub. 477:29. *pls. 21 & 22.* 1942.

Large tree to 25 m. tall. Twigs 1 to scarcely 2 mm. thick, fluted, from stellate-pubescent glabrate and brown with few rather inconspicuous light lenticels. Buds 2 to 2.5 mm. long, ovoid, subacute, glabrous, straw-colored; stipules caducous. Leaves evergreen, thin and hard, 10 to 15 cm. long, 4 to 6 cm. broad, broadly

lanceolate to oblanceolate, long-acuminate, the bases cuneate to rounded or apparently truncate and then minutely cuneate, entire or the margins slightly wavy but scarcely toothed, somewhat crisped, minutely revolute, both surfaces glabrous or sparsely stellate-pubescent at the base of the midrib above, dully shining; veins 12 to usually 15 or 18 on each side with evanescent intermediates, branching (often doubly) and anastomosing toward the margin, impressed above but slightly raised (as is the reticulum) within the grooves, quite prominent beneath, the reticulum less so; petioles about 4 mm. long (excluding the decurrent lamina), 1.5 to 3 mm. thick, glabrous or sparingly stellate-pubescent, dark reddish-brown. Staminate catkins? Pistillate catkins up to 1.5 cm. long, 2- or 3-flowered, the peduncle glabrous. Fruit annual, solitary, in twos, or in threes, peduncles about 1 cm. long, glabrous; cups about 25 mm. broad, 15 mm. high, cup-shaped, the scales ovate to ovate-lanceolate, basally thickened and densely gray-tomentose, the thin loose apices glabrous and reddish-brown; acorns about 25 mm. long, 16 to 18 mm. broad, ovoid, glabrous and light brown, the cotyledons decidedly unequal with the radicle lateral or equal with the radicle apical.

Quercus panamandinaea (named for Panama and *Andinae*, a series of black oaks which it superficially resembles quite closely) is a remarkable endemic species. It has no close relatives in Panama and is readily distinguished by the character of its cup scales and by its large, entire, long-acuminate, short-petioled leaves.

CHIRIQUÍ: Casita Alta to Copete, *Woodson* and *Schery 360* (type).

6. QUERCUS COPEYENSIS C. H. Mull., U.S.D.A. Misc. Pub. 477:30. *pls. 31* & *32*. 1942.

Large tree to 15 m. in height or taller. Twigs moderate (2 to 3 mm.), somewhat fluted, strikingly yellowish-white, glabrous. Buds round-ovoid, about 3 mm. long, glabrous, brown, the stipules persistent for a time, about 7 mm. long, ligulate, glabrous. Leaves deciduous, thick and very firm, 4 to 6 or rarely 8 cm. long, 2.5 to 4 cm. broad, ovate to obovate or broadly elliptic, the apex broadly rounded or merely obtuse, base subcuneate to cordulate but usually rounded, entire, the margins minutely revolute or flat, upper surfaces shiny, glabrous, lower surface dull, glabrous except occasional fulvous-stellate tomentum along the midrib toward the base; veins 6 or 7 or rarely 9 on each side, very irregular, much branched and obviously anastomosing, very slightly raised above with the reticulum not evident, more prominent beneath, the reticulum somewhat raised or not; petioles 4 to 7 mm. long, dark brown, glabrous. Staminate catkin 3 or 4 cm. long, the rachis sparsely pubescent or glabrous, loosely flowered or rather densely so toward the apex, the anthers little exserted. Pistillate catkins 2 or 3 cm. long, several-flowered toward the apex, the styles short, stigmas abruptly dilated if at all. Fruit annual, several distally grouped on a glabrous peduncle about 3 cm. long and 2 mm. thick; cups about 10 or 12 mm. broad, cup-shaped, the scales narrowly ovate, apically narrowed but obtuse, somewhat thickened basally, the thin apices closely appressed, gray-puberulent only at the base, otherwise glabrous and reddish-brown; acorns (immature) about 1 cm. in diameter, round, one-half included.

Quercus copeyensis is not closely related to any other species in Panama. It is readily distinguished from the other species of LEPIDOBALANUS by its small, relatively broad leaves. The species occurs also in central Costa Rica where it attains immense size.

CHIRIQUÍ: Volcán Chiriquí, between Potrero Muleto and the summit, *Woodson* and *Schery 383*.

7. QUERCUS HUMBOLDTII Bonpl. in Humb. & Bonpl., Pl. Aequinoct. 2:155. *pl. 130*. 1809.

Erythrobalanus humboldtii Schwarz, Notizbl. Bot. Gart. Mus. Berlin-Dahlem 13:496. 1937.

Medium-sized or large tree. Twigs 2 to 4 or rarely 7 mm. thick, fluted or subterete, from loosely fulvous-tomentose quickly or tardily becoming glabrate, the numerous light lenticels raised and very prominent. Buds about 5 mm. long, ovoid or elongating and acute, from loosely tomentose becoming glabrate and dull brown but the scales ciliate; the ligulate stipules rather early caducous. Leaves subevergreen or clearly evergreen, rather thin but hard and coriaceous, 10 to 20 cm. long, 3 to 7 cm. broad, lanceolate to elliptic or oblanceolate, acute or long-acuminate at apex, cuneate to rounded at base, entire or rarely coarsely few-toothed near the apex, margins minutely cartilaginous-revolute, flat or minutely crisped, upper surface glabrous and somewhat shining or the base of the midrib persistently tomentose, lower surface glabrate or rather persistently floccose especially along the midrib, opaque or somewhat shining, not bullate; veins about 12 to 16 on each side, branching and very obviously anastomosing near the margin, impressed above but slightly raised within the grooves, very prominent beneath, the reticulum rather inconspicuously raised beneath, less so above; petioles 4 to 10 or 15 mm. long, glabrate or persistently tomentose. Staminate catkins 8 to 15 cm. long, rather loosely flowered, the rachis sparsely villous, the obtuse anthers well exserted from the villous perianth. Pistillate catkins about 1 cm. long, 1- to 2-flowered. Fruit annual, solitary or paired on a peduncle 3 to 10 mm. long and 3 to 6 mm. thick with prominent lenticels; cups 2 to 3 cm. broad, deeply or shallowly cup-shaped, the margins inrolled or not, the scales narrowly ovate, obtuse, rather loosely appressed, short-fulvous-tomentose; acorns 2 to 3 cm. long, 1.5 to 2 cm. broad, round or ovoid, from loosely silky-tomentose becoming glabrate and brown, one-half or usually one-third included.

Quercus humboldtii is readily distinguished from the other species in Panama by its rather large entire lanceolate leaves and its large cups with loosely appressed thin scales. It is not closely related to any other species in Panama; its center is in the Andes of Colombia, where it is the only South American species of the genus. Its existence in Panama is attested by a single specimen in the New York Botanical Garden Herbarium labeled merely "Panama, 1859–1860." It is very likely that this specimen was taken in lower Panama near Colombia since no others of this species have turned up in the recent extensive explorations of the Chiriquí region.

DARIÉN (?): without specific locality data, *Hayes 830*.

8. Quercus seemannii Liebm., Overs. Danske Vidensk. Selsk. Forhandl. 1854: 188. 1854.

Quercus boquetensis Standl., Field Mus. Bot. Ser. 22:13. 1940.
Q. chiriquiensis Trel. ex C. H. Mull., U.S.D.A. Misc. Pub. 477:57. 1942. (as synonym).

Small or moderately large tree. Twigs 1 to 2.5 mm. thick, fluted, from sparsely pubescent soon glabrate and dark reddish-brown with prominent light lenticels. Buds 2 to 4 mm. long, ovoid or elongating, acute, glabrous, light brown; the ligulate stipules soon caducous. Leaves subevergreen, thin but rather hard, 4 to usually 8 or even 16 cm. long, 1 to usually 3 or 4 cm. broad, lanceolate or occasionally linear-lanceolate or ovate lanceolate or elliptic, apex long- or short-acuminate, base rounded to usually cuneate or attenuately acute, entire, margins minutely revolute, usually finely crisped, upper surface glabrate and shiny, lower surface glabrate or persistently tomentose along the midrib, dull; veins 8 to usually 10 or 12 on each side, repeatedly branching but obscurely anastomosing near the margin, very slightly or rather clearly raised above, or slightly impressed, somewhat more prominent beneath, the reticulum slightly raised on both surfaces; petioles 5 to usually 10 or rarely even 17 mm. long, rather prominently winged, glabrate. Staminate catkins 4 or 5 cm. long, rather loosely flowered, sparsely crisped-villous, the apiculate anthers slightly exserted. Pistillate catkins about 1 cm. long, 2- to 4-flowered along a slender glabrate peduncle. Fruit annual, rather small, solitary or paired on a peduncle 2 to 10 mm. long and as much as 3 mm. thick; cups goblet-shaped or deeper, 12 to 14 mm. broad, about 5 to 10 mm. high, the scales triangular-ovate, apices rounded, appressed, minutely sericeous-puberulent but the apices and margins glabrate and glossy brown; acorns about 12 to 15 mm. long, 11 or 12 mm. broad, subrotund to ovoid, loosely buff-puberulent, light brown where abraded, about one-fourth or one-third included; abortive ovules basal or lateral to subapical.

Quercus seemannii is rather similar to *Q. baruensis;* it is distinguished from that species by its thin blades, small leaves, and generally smaller fruit. *Q. seemannii* occurs commonly in Costa Rica.

chiriquí: labeled "Veraguas" and without further locality, *Seeman s. n.* (type); Cerro Vaca, eastern Chiriquí, *Pittier 5305*; Distr. de Boquete, Volcán Chiriquí, *Davidson 909*; vicinity of Casita Alta, Volcán Chiriquí, *Woodson, Allen,* and *Seibert 796* and *868*; Camiseta, Volcán Chiriquí, *Terry 1337*; Boquete, *Davidson 677* and *780* (type of *Q. boquetensis*); Salto Boquete, *Terry 1258*; Bajo Chorro, *Davidson 437* and *721*; upper valley of Río Chiriquí Viejo, between Paso Ancho and Monte Lirio, *Allen 1595*; between Finca Lérida and Peña Blanca, *Woodson* and *Schery 318*.

9. Quercus gulielmi-treleasei C. H. Mull., U.S.D.A. Misc. Pub. 477:58. *pls. 79* & *80*. 1942.

Quercus chiriquina Trel. ex C. H. Mull., U.S.D.A. Misc. Pub. 477:58. 1942. (as synonym).

Large tree. Twigs 1.5 to 3 mm. thick, fluted, from fulvous-stellate-tomentose becoming glabrate or sparsely floccose, reddish-brown with rather prominent pale lenticels, becoming gray. Buds about 2 mm. long, round to narrowly ovate, obtuse, straw-colored, glabrous or the scales minutely ciliate, the ligulate stipules

early caducous. Leaves deciduous (?), thin but firm and coriaceous, 8 to usually 18 or even 25 cm. long, 2 to usually 5 or sometimes 7 cm. broad, narrowly or broadly lanceolate to oblanceolate, apex narrowly acute to long-acuminate, not strikingly aristate-tipped, base cuneate to very narrowly rounded, entire, margins minutely revolute and very finely crisped, upper surface glabrous and shiny, lower surface glabrous or usually sparsely stellate-pubescent along the midrib toward the base, somewhat shining; veins about 15 to 18 or 20 on each side with evanescent intermediates, repeatedly branching and inconspicuously anastomosing near the margin, very slightly impressed above but somewhat raised within the grooves, rather prominent beneath, the fine reticulum somewhat raised on both surfaces; petioles 2 to 4 mm. long, as much as 2 mm. thick, winged, glabrate or pubescent like the twigs, dark reddish-brown at the swollen base. Catkins? Fruit probably annual, solitary or paired or several scattered on a peduncle 1 to 2 or 4 cm. long, 1.5 to 3 mm. thick, often irregularly bent in a zigzag at the points of attachment of the cups, glabrate, reddish-brown with conspicuous lenticels; cups 13 to 18 mm. broad, 5 to 10 mm. high, deeply saucer-shaped to goblet-shaped, often somewhat constricted at the base, the scales broadly triangular-ovate, rounded at apex, thin and very closely appressed, the base sometimes appearing thickened but merely protruded by the bud in its axil, finely buff-sericeous but the apices and margins glabrate; acorns 7 to 15 mm. long, 11 to 15 mm. broad, hemispheric to broadly ovate, apex nearly flat or rounded, from minutely sericeous-puberulent tardily glabrate, one-fifth included to completely covered (in equally mature material, varying with the form of the acorn); abortive ovules basal.

Quercus gulielmi-treleasei is not very closely related to *Q. seemanii,* its closest ally, but aside from the larger leaves, very short petioles, and rather longer-stalked, smaller fruit of the former, distinguishing characters are difficult to ascertain. Such a paucity of distinctions characterizes the whole group of entire-leafed black oaks of the tropics and subtropics, especially if fruiting material is not available. *Q. gulielmi-treleasei* occurs also in Costa Rica.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 226* (type); between Boquete and Finca Lérida, *Allen 302.*

10. QUERCUS BARUENSIS C. H. Mull., Trop. Woods 108:75. 1958.

Tree to 30 m. tall, the trunk to 1.8 m. in diameter. Twigs 2 to 3 mm. in diameter, nearly glabrous or densely stellate-tomentulose, soon or tardily glabrate with inconspicuous light lenticels, gray the second year and the lenticels numerous and more prominent (this variation occurring as polymorphism of individual trees). Buds 2 to 3 mm. long, ovoid, apically rounded, dull straw-colored, the scales markedly ciliate or glabrate; stipules quickly caducous (not seen). Leaves deciduous (?), firm and coriaceous, 10 to 15 cm. long, 2.5 to 6 cm. broad, entire, lanceolate or ovate-lanceolate, acuminate, the ultimate apex not aristate, cuneate to obtuse at base, blades dull green and glabrate above or sparingly stellate pubescent along the base of the midrib, very dull beneath, the midrib and veins persist-

ently stellate-tomentose, especially in the axils, margins nearly flat, minutely cartilaginous; veins about 8 to 10 on each side, obviously branching and anastomosing toward the margin, minutely raised on the upper surface, rather prominently raised on the lower surface; petioles 8 to 18 mm. long, winged by the decurrent blade, the upper surface flattened, pubescent or glabrate like the twigs. Flowers not seen. Fruit annual, solitary (from short multiflowered catkins) on short, thick peduncles 3 to 10 mm. long and 3 to 5 mm. thick; cups 13 to 17 mm. broad, 8 to 10 mm. deep, cup-shaped, the bases rounded, the margins not inrolled, the scales tightly appressed, prominently tan-puberulent all over; acorns about 10 mm. long and 15 mm. broad, densely puberulent, about two-thirds included.

Quercus baruensis is distinguished from *Q. gulielmi-treleasei* by its long petioles and thick leaf blades and from *Q. seemannii* by its much larger leaves and fruit. Although the species may occur in Costa Rica, it is thus far known only in Panama.

CHIRIQUÍ: north of El Hato, Volcán Baru, *Stern* and *Chambers 55* (type); Cerro Punta, *Stern* and *Chambers 76*; *Allen 3496* and *3523*; Llano del Volcán, *Allen* and *Fairchild 3464* and *3467*.

ULMACEAE

By LORIN I. NEVLING, Jr.

Bisexual, monoecious or dioecious shrubs or trees, sap watery. Leaves simple, mostly alternate but sometimes opposite, often distichous, often inequilateral; petiolate; stipules lateral or interpetiolar, caducous. Inflorescences solitary, cymose or in axillary fascicles, borne on previous or current year's growth. Flowers bisexual or unisexual by abortion, anemophilous, obscurely zygomorphic; sepals 4–8, free or basally connate; petals 0; stamens generally equal to or twice, rarely more than twice, as many as the sepals, erect in bud, the anthers 2-celled, dehiscing longitudinally; pistil 1, rudimentary in staminate flowers, in pistillate and bisexual flowers the ovary superior, sessile or stipitate, 2-carpellate, 1-locular or rarely 2-locular, the ovule 1, anatropous, pendulous from locule apex, the styles 2, free or fused at the base, linear, stigmatose on upper inner surface; fruit a more or less winged samara with straight embryo and flat cotyledons or a drupe with curved embryo and rolled or folded cotyledons.

A widely distributed family of approximately 15 genera and more than 160 species.

a. Fruit more or less samaroid, dry; seed flat; embryo straight with generally flat cotyledons, exendospermous.......... 1. Ulmus
aa. Fruit drupaceous; seed round; embryo curved with folded or rolled cotyledons; endosperm sometimes present.
  b. Leaves opposite; stipules interpetiolar.......... 2. Lozanella
  bb. Leaves alternate; stipules lateral.
    c. Stamens as many as the sepals.
      d. Pistillate flowers in lax, many-flowered cymes; plants unarmed. 3. Trema
      dd. Pistillate flowers solitary or few; plants often armed.......... 4. Celtis
    cc. Stamens at least twice as many as the sepals.......... 5. Ampelocera

1. ULMUS L.

Ulmus L. Sp. Pl. 225. 1753.

Microptelea Spach, in Ann. Sc. Nat. Ser. 2. 15:358. 1841.
Chaetoptelea Liebm. in Kjoeb. Vidensk. Meddel. 76. 1850.

Bisexual shrubs or trees, the branches often flexuose. Leaves alternate, distichous, inequilateral, serrate; stipules lateral. Inflorescence racemose or fasciculate, borne axillary on last year's growth. Flowers bisexual; sepals 4–8, more or less connate at the base; stamens as many as and opposite the calyx lobes, the anther dehiscence extrorse; ovary sessile or stipitate, 2-carpellate, 1-locular, compressed, the styles 2, often introrsely recurved, persistent. Fruit more or less samaroid, dry; seed flat; embryo straight with generally flat cotyledons; exendospermous.

Represented in Panama by a single species.

1. Ulmus mexicana (Liebm.) Planch. in DC. Prodr. 17:156. 1873.

Chaetoptelea mexicana Liebm. in Kjoeb. Vidensk. Meddel. 77. 1850.

Trees to 25 m. tall, the young branches sparsely hirsute to glabrous. Leaves

Fig. 31. *Ulmus mexicana*

lanceolate- to ovate-elliptic, 4–16 cm. long, 2–7 cm. broad, acute to attenuate at the apex, only the costa pubescent above, glabrous to puberulent below, serrate; petiole 4–10 mm. long, glabrous to sparsely hirsute. Inflorescence racemose, to 6 cm. long. Flowers with pedicel to 5 mm. long, hirsute; tepals 5, connate into a more or less campanulate tube, white; stamens 5, exserted, the filaments about 3.5 mm. long, the anthers about 0.75 mm. long, 1 mm. broad; ovary obovate, velutinous on margins, borne on a cuneate gynophore, the styles introrsely recurved, papillose stigmatic surface. Fruit obovate, 9–11 mm. long, 2.5–3.0 mm. broad; seed about 1.75 mm. long, 1.25 mm. broad.

Mexico to Panama.

CHIRIQUÍ: Río Chiriquí Viejo, 3 kilometers n. of Camp El Volcán, *Little 6060, 6074, 6076*; trail from Paso Ancho to Monte Lirio, upper Río Chiriquí Viejo, alt. 1500–2000 m., *Allen 1591*; Boquete, el. 5500 ft., *Davidson 533*.

2. LOZANELLA Greenm.

LOZANELLA Greenm. in Proc. Amer. Acad. 41:236. 1905.

Dioecious trees. Leaves opposite, slightly inequilateral, serrate, long-petiolate; stipules interpetiolar. Inflorescence many-flowered, cymose, axillary, bracteolate, borne on current year's wood. Staminate flowers: shortly pedicellate; sepals 5 (–6), more or less connate at the base; stamens as many as and opposite the calyx lobes, disc present; pistil rudimentary. Pistillate flowers: sessile; perianth as in staminate flowers; staminodes 0; pistil 1, the ovary sessile, 2-carpellate, 1-locular, the styles 2, spreading, persistent. Fruit a small drupe, the embryo and cotyledons only slightly curved.

Two species, only one found in Panama. Mexico to Bolivia.

Fig. 32. *Lozanella enantiophylla*

1. Lozanella enantiophylla (Donn. Sm.) Killip & Morton, in Journ. Wash. Acad. Sci. 21:339. 1931.

Trema enantiophylla Donn. Sm. in Bot. Gaz. 33:259. 1902.
Lozanella trematoides Greenm. in Proc. Amer. Acad. 41:236. 1905.

Tree to 10 m. tall, the stems terete or slightly compressed at the nodes, young branches densely villous, mature branches glabrate with elliptic, white lenticels. Leaves ovate to ovate-lanceolate, 8–16 cm. long, 3–9 cm. broad, acuminate, obtuse or acute at the base, scabrous and hirsute above, hirsute below, serrate; petiole 1–4 cm. long. Staminate flowers: sepals 5(–6), 1.5–2.5 mm. long, connate at the base, margin ciliate, green; stamens exserted, the filaments broadly filiform, glabrous, the anthers about 1.25 mm. long, 1 mm. broad, subversatile, the disc minute, pilose; ovary rudimentary, about 1 mm. long. Pistillate flowers: perianth as in staminate flower; staminodes 0; fruit subglobose, approximately 2 mm. in diameter, orange.

Mexico to Peru.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, ca. 1500–2000 m., *Woodson, Allen & Seibert 841*; Quebrado Velo, alt. 1800 m., *Woodson & Schery 256*; valley of the upper Río Chiriquí Viejo, *P. White 344*; trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt. 1500–2000 m., *Allen 1505*.

3. TREMA Lour.

Trema Lour. Fl. Cochinch. 562. 1790.

Sponia Comm. ex Lam. Encycl. 4:139. 1796.

Bisexual or monoecious trees or tall shrubs. Leaves alternate, distichous, more or less inequilateral, mostly serrate, shortly petiolate; stipules lateral. Inflorescences solitary, cymose or fasciculate. Bisexual flowers: sepals 4–5, connate at the base; stamens as many as and opposite the calyx lobes, anther dehiscence introrse; ovary sessile, 1-locular, the styles connate below. Staminate flowers with rudimentary pistil. Pistillate flowers without staminodes. Fruit a small ovoid or subglobose drupe with persistent styles, the embryo curved, the cotyledons falcate, thick.

A genus of highly variable taxonomically confused species. Widely distributed in subtropical and tropical regions. A single species found in Panama.

1. Trema micrantha (L.) Blume, in Ann. Mus. Bot. Lugd. Bat. 2:58. 1853.

Rhamnus micranthus L. Syst. Nat. ed. 10. 2:937. 1759.
Celtis mollis Humb. & Bonpl. ex Willd. Sp. Pl. 4^2:996. 1806.
Celtis rugosa Willd. loc. cit. 1806.
Celtis canescens HBK. Nov. Gen. & Sp. 2:28. 1817.
Celtis riparia HBK. loc. cit. 1817.
Celtis macrophylla HBK. loc. cit. 30. 1817.
Celtis schiedeana Schlecht. in Linnaea 7:140. 1832.
Sponia micrantha (L.) Decne. in Nouv. Ann. Mus. Par. 3:498. 1834.
Sponia mollis (Humb. & Bonpl. ex Willd.) Decne. loc. cit. 1834.
Sponia canescens (HBK.) Decne. loc. cit. 1834.
Sponia riparia (HBK.) Decne. loc. cit. 1834.
Sponia macrophylla (HBK.) Decne. loc. cit. 1834.

Fig. 33. *Trema micrantha*

Sponia lima Decne. loc. cit. 1834.
Sponia schiedeana (Schlecht.) Planch. in Ann. Sc. Nat. Sér. 3. 10:335. 1848.
Celtis microcarpa Salzm. ex Planch. loc. cit. 333. 1848.
Celtis rufescens Banks, ex Planch. loc. cit. 334. 1848.
Celtis chichilea Ruiz & Pav. ex Planch. loc. cit. 335. 1848.
Sponia crassifolia Liebm. in Vidensk. Selsk. Skr. 5^2:340. 1851.
Sponia grisea Liebm. loc. cit. 1851.
Trema canescens (HBK.) Blume, loc. cit. 1853.
Trema schiedeana (Schlecht.) Blume, loc. cit. 1853.
Trema lima (Decne.) Blume, loc. cit. 1853.
Trema riparia (HBK.) Blume, loc. cit. 1853.
Trema mollis (Humb. & Bonpl. ex Willd.) Blume, loc. cit. 1853.
Trema macrophylla (HBK.) Blume, loc. cit. 1853.
Trema chichilea (Ruiz & Pavon, ex Planch.) Blume, loc. cit. 1853.
Trema rufescens (Banks, ex Planch.) Blume, loc. cit. 1853.
Trema melinona Blume, loc. cit. 64. 1853.
Sponia integerrima Beurl. in Vet. Akad. Handl. Stockh. 1854:144. 1856.
Celtis lima (Decne.) Sw. Prod. 53. 1888.
Trema micrantha var. *obtusatum* Urb. Symb. Ant. 4:195. 1905.
Trema integerrima (Beurl.) Standl. in Contrib. Arn. Arb. 5:55. 1933.
Trema strigillosa Lund. in Phytologia 1:337. 1939.
Trema micrantha var. *strigillosa* Standl. & Steyerm. in Fieldiana Bot. 24^4:9. 1946.

Monoecious trees to 20 m. tall, the young branches flexuose, villous; stipules

narrowly lanceolate. Leaves lanceolate to ovate-elliptic, 5–17 cm. long, 1.5–7.0 cm. broad, attenuate at the apex, hirsute and scabrous above, sparsely to densely villous below, serrate or entire; petiole 0.5–1.8 cm. long, villous. Flowers small, subsessile, bracteolate. Staminate flowers: sepals 5, 0.75–1.0 mm. long, hirsute on outer surface; stamens 5, torus hairy; pistillode more or less cylindrical, about 0.5 mm. long, 0.5 mm. in diameter. Pistillate flowers: perianth as in staminate flowers; staminodes 0; the ovary globose, strigose toward the apex, the styles two, fused at the base. Fruit ovoid or subglobose, 3–4 mm. long, around 3 mm. in diameter, red, malodorous.

An extremely variable species which has been variously divided in the past. Very common in Panama on cut over land.

BOCAS DEL TORO: Water Valley, *von Wedel 867, 1624, 1791*; Changuinola Valley, *Cooper & Dunlap 18, Dunlap 442*; Changuinola Valley, Lincoln Creek, *Dunlap 431*. CANAL ZONE: two miles below Madden Dam, *Bro. Maurice 821*; south of island, *P. White 110*; vicinity of Miraflores Lake, *G. White 153*; Fort Kobe Road, *Woodson, Allen & Seibert 1409*; France Field, Colon, *Riley 101*; Barro Colorado Island, *Aviles 58*. CHIRIQUÍ: vicinity of San Bartolomé, Peninsula de Burica, alt. 0–50 m., *Woodson & Schery 911*; vicinity of Chiriquí Lagoon, Old Bank Island, *von Wedel 2117*; Río Chiriquí to Remedios, ca. 15–50 m., *Woodson, Allen & Seibert 1190*; vicinity of Río Tinta, along main highway, *Woodson, Seibert & Allen 410*; trail from Paso Ancho to Monte Lirio, upper valley Río Chiriquí Viejo, alt. 1500–2000 m., *Allen 1485*; Boquete, Volcán de Chiriquí, 7000 ft., *Davidson 924*; Boquete, Bajo Mono, el. 4500 ft., *Davidson 485*; vicinity of Casita Alta, Volcán de Chiriquí, ca. 1500–2000 m., *Woodson, Allen & Seibert 917*; vicinity of Finca Lérida, alt. 1750 m., *Woodson & Schery 208*; forested ridges south of Finca Lérida, alt. 6000–7000 ft., *Allen 4760*; vicinity of Puerto Armuelles, alt. 0–75 m., *Woodson & Schery 837*. COLÓN: vicinity of Camp Pina, alt. 25 m., *Allen 3670*. PANAMÁ: vicinity of Arenoso, lower Río Trinidad, 26–50 m., *Seibert 621*; Isla Taboga, ca. 0–186 m., *Woodson, Allen & Seibert 1543*; San José Island, Between Headquarters and Main Beach, *Johnston 1191, 1192*; San José Island, M-area road, edge of forest, *Johnston 269*. SAN BLAS: *Cooper 289*.

4. CELTIS L.

CELTIS L. Sp. Pl. 2:1043. 1753.

Mertensia HBK. Nov. Gen. & Sp. 2:30. 1817, non L.
Momisia F. G. Dietr. in Vollst. Lexik. Gaertn. Nachtr. 5:122. 1819.
Saurobroma Raf. Sylva Tellur. 32. 1838.
Solenostigma Endl. Prod. Fl. Norf. 41. 1833.

Polygamo-monoecious or monoecious shrubs or trees, unarmed or with spinose branches. Leaves alternate, distichous, often inequilateral, serrate or entire; petiolate; stipules lateral. Inflorescences borne on this year's wood: staminate inflorescence cymose or fasciculate, pistillate inflorescence solitary or few-flowered fasciculate. Flowers small, pedicellate. Bisexual flowers: sepals 4–5, more or less connate at the base; stamens as many as and opposite the calyx lobes, the anther dehiscence extrorse, disc present; ovary sessile, 1-locular, the styles 2, sometimes united at the base, reflexed. Staminate flowers with rudimentary pistil. Pistillate flowers without staminodes. Fruit an ovoid or subglobose drupe, the embryo curved, the cotyledons broad, conduplicate or rarely flat, variously folded.

Fig. 34. *Celtis iguanaeus*

Approximately 75 species, widely distributed in temperate and tropical regions. Only 1 represented in Panama.

1. Celtis iguanaeus (Jacq.) Sarg. Silv. N. Amer. 7:64. 1895.

Rhamnus iguanaeus Jacq. Enum. Pl. Carib. 16. 1762.
Celtis aculeata Sw. Prod. Veg. Ind. Occ. 53. 1788.
Zizyphus iguanea (Jacq.) Lam. Dict. 3:318. 1789.
Celtis epiphylladena Orteg. Hort. Matr. 79. 1800.
Celtis rhamnoides Willd. Sp. Pl. 4:998. 1806.
Mertensia laevigata HBK. Nov. Gen. & Sp. 2:31, *t. 103*. 1817.
Mertensia zizyphoides HBK. loc. cit. 1817.
Momisia laevigata (HBK.) F. G. Dietr. Vollst. Lexik. Gaertn. Nachtr. 5:123. 1819.
Momisia zizyphoides (HBK.) F. G. Dietr. loc. cit. 124. 1819.
Zizyphus commutata Roem. & Schult. Syst. Veg. 5:336. 1819.
Mertensia iguanea (Jacq.) Schult. Syst. Veg. 6:312. 1820.
Mertensia rhamnoides (Willd.) Schult. loc. cit. 313. 1820.
Celtis laevigata (HBK.) Spreng. Syst. 1:932. 1825.
Celtis glabratum Spreng. Syst. 5:150. 1828.

Momisia ehrenbergiana Klotzsch, in Linnaea 20:538. 1847.
Momisia aculeata (Sw.) Klotzsch, loc. cit. 539. 1847.
Celtis orthacanthos Planch. in Ann. Sc. Nat. Ser. 3. 10:309. 1848.
Celtis zizyphoides (HBK.) Planch. loc. cit. 314. 1848.
Celtis anfractuosa Liebm. in Vidensk. Selsk. Skr. Ser. 5. 2:338. 1851.
Celtis ehrenbergia (Klotzsch) Liebm. loc. cit. 339. 1851.
Celtis aculeata var. *pubescens* Griseb. Fl. Br. W. Ind. 149. 1861.
Celtis aculeata var. *serrata* Griseb. loc. cit. 1861.
Celtis aculeata β laevigata Planch. in DC. Prod. 17:187. 1873.
Mertensia commutata (Roem. & Schult.) Hemsl. Biol. Centr. Am. Bot. 3:138. 1882–86.
Celtis platycaulis Greenm. in Proc. Amer. Acad. 39:78. 1903.
Momisia iguanaea (Jacq.) Rose & Standl. in Contrib. U. S. Nat. Herb. 16:8. 1912.
Momisia anfractuosa (Liebm.) Rose & Standl. loc. cit. 1912.

Andromonoecious shrubs or small trees to 12 m. tall, the branches flexuose, armed with short recurved spines. Leaves ovate to broadly elliptic, 3–11 cm. long 1.5–4.5 cm. broad, acute or attenuate at the apex, obtuse to subcordate at the base, slightly inequilateral, 3-nerved at the base, sparsely pubescent to glabrous above and below, serrate at least toward the apex; petiole 0.5–1.0 cm. long. Inflorescence cymose, fasciculate. Bisexual flowers: sepals 5, about 1.5 mm. long, 0.75 mm. broad, connate at the base, margin ciliate, greenish-yellow; stamens 5, exserted, the filaments 1.5 mm. long, glabrous, the anthers 1 mm. long, 0.75 mm. broad, the torus hairy; ovary more or less cylindrical, shortly hairy, the styles 2, fused at the base. Staminate flowers with rudimentary pistil. Flowers described from Mexican specimens. Fruit ovoid, 8–12 mm. long, 6–8 mm. in diameter, yellow, orange or red.

Mexico to Argentina, and the Antilles.

CANAL ZONE: Barro Colorado Island, *Aviles 27b*.

5. AMPELOCERA Klotzsch

AMPELOCERA Klotzsch, in Linnaea 20:541. 1847.

Bisexual or andromonoecious trees, unarmed. Leaves alternate, slightly inequilateral, remotely serrate or entire, short-petiolate; stipules lateral. Inflorescence many-flowered fasciculate, axillary, borne on this year's wood. Bisexual flowers: sepals 5, fused at the base; stamens at least twice as many as the calyx lobes; ovary sessile, the styles 2, fused at the base, spreading, persistent. Staminate flowers with rudimentary pistil. Fruit a small drupe.

Five species, only 1 Central American, the remainder Antillean or South American.

1. AMPELOCERA HOTTLEI (Standl.) Standl. in Trop. Woods 51:11. 1937.

Celtis hottlei Standl. in Trop. Woods 20:20. 1929.

Apparently bisexual trees to 30 m. tall. Leaves elliptic-oblong, 7–13 cm. long, 3–6 cm. broad, glabrous, coriaceous, shortly attenuate at the apex, acute at the base, entire; petiole 0.3–0.6 cm. long. Inflorescence dense, at most only slightly exceeding the petiole of the subtending leaf in length. Flowers sessile, subtended by a pair of bracteoles; sepals 5, fused for about half of their length, cream;

Fig. 35. *Ampelocera hottlei*

stamens 10 or rarely more, exserted, the filaments about 2 mm. long, glabrous, the anthers 1.25 mm. long, 0.75 mm. broad, basifixed; styles persistent, stigmas bifid, divergent. Fruit globose, about 10 mm. long, 5 mm. in diameter, densely puberulent, yellow.

A Central American species found generally at low altitudes in well developed forests.

SAN BLAS: forest about Puerto Obaldía, *Pittier 4319*.

MORACEAE

Trees and shrubs, very rarely low herbs (*Dorstenia* spp.), more or less abundantly laticiferous; monoecious or dioecious. Leaves alternate, distichous or spiral, simple, entire to deeply lobed, basifixed or peltate (*Cecropia*), variously involute or convolute in vernation; stipules lateral or intrapetiolar, commonly amplexicaul. Flowers unisexual, monochlamydeous or naked, minute, commonly in racemes, spikes or heads, rarely in cymes, in *Ficus* enclosed within fleshy saccate axial receptacles (syconia). Stamens 1–4, the filaments involute or erect before anthesis, the anthers 1- to 2-celled, longitudinal or rarely circumscissile (*Brosimum* spp.) in dehiscence. Pistil 1- to 2-carpellate; ovary superior to inferior, 1-celled, containing a single erect to pendulous ovule. True fruit generally a drupe or an achene, but the perianth or the whole inflorescence becoming fleshy at maturity, as in the breadfruit (*Artocarpus*) and the fig (*Ficus*).

The family is very widely distributed throughout the warmer parts of the earth and supplies one of the most essential elements of a "typical" lowland landscape in the tropics. There are well over 1000 species, of which more than half are included within the familiar genus *Ficus*. This is a very fortunate circumstance for, with the exception of such well-known but smaller members as *Morus* and *Artocarpus*, the other genera are for the most part chaotically ill-defined. There can scarcely be an equally prominent family of flowering plants more in need of taxonomic revision than Moraceae, which have not had an inclusive monographer since Trécul and Miquel more than a century ago. Engler's treatment of the family for "Die natürlichen Pflanzenfamilien", derived from Bentham and Hooker, definitely lacks realism; *Trophis* and *Sorocea*, for example, which were placed in different subfamilies, possibly are congeneric. Although all genera reported from Panama are distinguished with some difficulty in the key which follows, probably less than a dozen natural groups actually exist.

a. Trees and shrubs.
  b. Leaves distichous; stipules lateral to fully amplexicaul.
    c. Pistillate flowers with a simple filiform lateral stigma, in dense globular heads; staminate flowers in elongate spikes with spatulate glandular-carinate bracts; stipules lateral, not leaving a scar completely surrounding the stem; leaves usually strongly inequilateral and more or less cordate at the base, closely serrate to entire; stems frequently with stout axillary spines .... 1. Chlorophora
    cc. Pistillate flowers with a central more or less prominently 2-lobed stigma.
      d. Both pistillate and staminate flowers in more or less elongate racemes or spikes (the pistillate flowers occasionally in axillary pairs or solitary in *Clarisia*), with small peltate bracts; stipules lateral to about half-amplexicaul, not leaving a scar completely surrounding the stems; leaves nearly or quite equilateral and cuneate to rounded at the base, entire to rather irregularly and remotely serrate; stems unarmed.
        e. Staminate inflorescences solitary or paired on separate peduncles, the flowers with an obvious perianth and 4 stamens; pistillate flowers without individual basal involucres.

f. Staminate flowers spicate or racemose, with an obvious pistillode, the stamens strongly inflexed before anthesis, the anthers introrse; pistillate flowers spicate or racemose, epigynous. .... 2. TROPHIS

ff. Staminate flowers racemose, without an obvious pistillode, the stamens scarcely inflexed before anthesis, the anthers extrorse; pistillate flowers racemose, perigynous........ 3. SOROCEA

ee. Staminate inflorescences usually 2–several on a common peduncle, the flowers with a vestigial perianth and a single stamen; pistillate flowers with inconspicuous but persistent individual basal involucres, epigynous........ 4. CLARISIA

dd. Both pistillate and staminate flowers in globose or discoid heads (the pistillate usually solitary in *Brosimum, Olmedia* and *Pseudolmedia*); stipules fully amplexicaul and leaving a scar completely surrounding the stem (except in *Batocarpus* and occasionally in *Brosimum*).

e. Inflorescences typically monoecious (occasionally dioecious) globose heads with 1–2 central pistillate flowers surrounded by innumerable minute staminate commingled with more or less conspicuous peltate bracts; stipules lateral or almost fully amplexicaul; unarmed trees........ 5. BROSIMUM

ee. Inflorescences dioecious, without peltate bracts.

f. Stipules lateral, not leaving a scar completely surrounding the stem; staminate heads discoid, involucrate; pistillate heads globose, without an involucre; unarmed trees........ 6. BATOCARPUS

ff. Stipules fully amplexicaul, leaving a scar completely surrounding the stem.

g. Pistillate heads with several fertile flowers; anthers oval, scarcely longer than broad.

h. Unarmed trees, pistillate heads with a definitely organized involucre; staminate heads discoid, with a definitely organized involucre.

i. Staminate heads flat or nearly so, the flowers definitely organized with 4 tepals and 4 stamens; pistillate flowers free and hypogynous; leaves entire to indefinitely serrate-undulate, glabrous to softly puberulent........ 7. PEREBEA

ii. Staminate heads more or less conduplicate-flabellate, with essentially unorganized flowers; pistillate flowers coherent at the base and perigynous; leaves closely and minutely ciliate-denticulate, scabrous to hispid........ 8. CASTILLA

hh. Aculeate trees; pistillate heads without a definite involucre; staminate heads globose, without an involucre; leaves entire to indefinitely undulate........ 9. POULSENIA

gg. Pistillate heads typically with a solitary prominently involucrate flower; anthers oblongoid, much longer than broad; unarmed trees.

h. Staminate flowers with a broadly campanulate perianth and 4 stamens; pistillate flowers hypogynous; leaves usually more or less serrate-undulate toward the tip.....10. OLMEDIA

hh. Staminate heads without organized flowers, the stamens commingled with prominent bracts and bracteoles; pistillate flowers perigynous or epigynous; leaves entire........11. PSEUDOLMEDIA

bb. Leaves spiral; stipules fully amplexicaul and leaving a scar completely surrounding the stem.

c. Flowers wholly contained within a more or less fleshy osteolate saccate predominantly monoecious receptacle; leaves of native species entire; stems mostly solid........12. FICUS

cc. Flowers external in spikes or cymes; plants dioecious; stems usually hollow.

d. Leaves basifixed, entire to palmately lobed.

e. Leaves typically palmately lobed (entire in some extra-Panamanian species); inflorescences repeatedly cymose, the flowers rather indefinitely glomerate at the ends of the branches; staminate flowers with 4 nearly free tepals and 4 separate stamens; pistillate flowers with a fleshy cupular perianth and an obscurely 2-lobed stigma; fruit a rather large false drupe. ....13. Pourouma

ee. Leaves entire to more or less definitely undulate or crenate towards the tip; staminate inflorescences dichotomously compounded small globular heads, the flowers with 4 more or less united tepals and 2 completely united stamens; pistillate inflorescences superficially simple or rather obscurely dichotomous heads, the flowers much as in *Cecropia*; fruit a small slightly fleshy drupe..14. Coussapoa

dd. Leaves peltate, palmately lobed (or compound in some extra-Panamanian species); both staminate and pistillate inflorescences of spadicose spikes in digitate clusters, the perianths tubular with thin shredding walls and a fleshy porous operculum, the stamens 2, the stigma penicillate, barely exserted; fruit a minute slightly fleshy drupe..15. Cecropia

aa. Succulent subacaulescent herbs (our species); leaves spiral; stipules lateral; plants monoecious; staminate and pistillate flowers minute, interspersed and immersed in a common discoid or radiate head...............16. Dorstenia

The genus *Ogcodeia* occurs in Costa Rica and may yet be found in Panama. It is related to *Perebea* and *Helicostylis*, but is distinguished by the burr-like pistillate inflorescences and fruits; the heads are involucrate as in *Perebea* but the flowers epigynous and reduced in number as in *Helicostylis*.

The East Indian and Micronesian genus *Artocarpus* is represented in cultivation by the breadfruit (*A. communis* Forst.) and the jackfruit (*A. heterophyllus* Lam.). Both are large and handsome shade trees and are monoecious, the staminate flowers in stout cylindrical spikes and the pistillate in great spherical or cylindrical heads somewhat reminiscent of the northern Osage orange [*Maclura pomifera* (Raf.) Schneid.] on a larger scale. The jackfruit has undivided leaves; breadfruit leaves are leathery, deep glossy green and incised like those of some monstrous oak. Breadfruit, which was the principal cargo of the ill-fated H.M.S. "Bounty" in 1789, still is an important article of food for many people in Panama, both for the starchy pulp of the fruit and for the large nut-like seeds of some varieties (breadnuts); by the Spanish-speaking people it is known as *árbol de pan* and *fruta de pan*. Jackfruits are edible but of inferior quality.

1. CHLOROPHORA Gaud.

Chlorophora Gaud. Bot. Voy. Freycinet 509. 1830.

Dioecious trees, the branches occasionally with stout axillary spines. Leaves alternate, distichous; stipules lateral and about half-amplexicaul. Inflorescences axillary, the staminate spicate, the pistillate capitate; flowers associated with spatulate glandular-carinate bracts. Staminate flowers with 4 essentially free tepals; stamens 4, the filaments rather elongate, involute before anthesis, the anthers 2-celled, extrorse. Pistillate flowers with 4 basally coherent tepals, hypogynous, the pistil with a simple filiform lateral stigma. Fruit a loosely coherent slightly fleshy syncarp.

Two species—the following and *Ch. excelsa* (Welw.) Benth. & Hook. f. of western tropical Africa.

Fig. 36. *Chlorophora tinctoria*

1. Chlorophora tinctoria (L.) Gaud. Bot. Voy. Freycinet 508. 1830.

Morus tinctoria L. Sp. Pl. 986. 1753.
Morus xanthoxylon L. Syst. Nat. ed. 10. 2:1267. 1759.
Broussonetia tinctoria (L.) HBK. Nov. Gen. & Sp. 2:32. 1817.
Broussonetia plumerii Spreng. Syst. Veg. 3:901. 1826.
Morus tataiba Vell. Fl. Flum. 10: *t. 21.* 1827.
Maclura tinctoria (L.) D. Don, ex Steud. Nomencl. ed. 2. 2:87. 1841.
Maclura plumiera D. Don, ex Steud. loc. cit. 1841.
Morus plumiera (D. Don) Burm. ex Steud. loc. cit. 1841.
Broussonetia xanthoxylon (L.) Mart. in Flora 24: 2 Beibl. 10. 1841.
Broussonetia brasiliensis Mart. loc. cit. 1841.
Maclura sempervirens Ten. Cat. Hort. Bot. Nap. 87. 1845.
Maclura xanthoxylon (L.) Endl. Gen. Pl. Suppl. 4^2:34. 1847.
Maclura chlorocarpa Liebm. in Danske Vidensk. Selsk. Skr. 5 ser. 2:314. 1851.
Maclura polyneura Miq. in Mart. Fl. Bras. 4^1:154. 1853.
Maclura affinis Miq. loc. cit. 155. 1853.
Maclura subintegerrima Miq. loc. cit. 157. 1853.
Maclura velutina Bl. Mus. Bot. Lugd.-Bat. 2:82. 1856.
also numerous infraspecific epithets.

Trees, reputedly to 30 m. in height. Leafy twigs rather slender, somewhat flexuose, glabrous, developing a yellowish gray bark. Leaves alternate, distichous, petiolate, the blade quite variable, broadly oval to ovate, obovate or oblong, the tip usually subcaudate-acuminate, the base usually strongly inequilateral and more or less cordate, closely serrate to entire, 3–12 cm. long, 2–6 cm. broad, firmly membranaceous, glabrous to minutely puberulent above and below, the petiole 5–10 mm. long, slender; stipules lateral, leaving a scar about half-surrounding the stem or less, narrowly lanceolate, 2–10 mm. long. Staminate spikes slender, 3–10 cm. long, bearing innumerable densely congested flowers interspersed with minute puberulent spatulate glandular-carinate bracteoles about 6 mm. long: tepals 4, broadly oval, minutely puberulent, about 3 mm. long; stamens 4, the filaments about 5 mm. long, strongly involute before anthesis, the anthers broadly oval, about 1.5 mm. long; pistillode about 1 mm. long. Pistillate heads globose, about 1 cm. in diameter, very shortly pedunculate, the flowers very densely congested and interspersed with spatulate glandular-carinate bracteoles about 6 mm. long: tepals 4, narrowly spatulate, about 6 mm. long, minutely puberulent; ovary superior, obovoid, about 4 mm. long, the lateral filiform densely papillate stigma about 10 mm. long. Fruit a very slightly fleshy, globose aggregate to about 2 cm. in diameter.

Southern Mexico to Argentina; Antilles, at low elevations. *Mora* or *morillo* and *macano*; fustic. The wood is extremely durable and resistant to insects and decay according to Allen (Allen, P. H. The Rainforests of Golfo Dulce. Gainesville, Fla. 1956).

canal zone: between France Field and Catival, *Standley 30301*; Balboa Heights, *Killip 3000*; Darién Sta., *Standley 31600*. chiriquí: Puerto Armuelles, *Woodson & Schery 899*, *Stern & Chambers 136*; Progreso, *Cooper & Slater 237*. darién: Garachiné, *Pittier 5695*. panamá: Las Sabanas, *Zetek 3684*; Panamá, *Standley 26833*; Río Tapía, *Standley 28200*; Río Tecumen, *Standley 29381*; Chepo, *Pittier 4710*.

2. TROPHIS P. Br.

TROPHIS P. Br. Hist. Jam. 357. 1756; L. Syst. Nat. ed. 10. 1289. 1759, nom. conserv.

Bucephalon L. Sp. Pl. 1190. 1753, nom. rejic.
Skutchia Pax & Hoffm. ex Morton, in Journ. Wash. Acad. Sci. 27:306. 1937.

Dioecious trees and shrubs, the branches unarmed. Leaves alternate, distichous; stipules lateral. Both staminate and pistillate inflorescences secund racemes and spikes, the small congested or relatively distant flowers interspersed with small, shortly stipitate, peltate bracts. Staminate flowers: tepals 4, united or essentially free to the base, with an obvious pistillode; stamens 4, the filaments much longer than the tepals and strongly inflexed before anthesis, later sharply reflexed, the anthers broadly oval, introrse. Pistillate flowers epigynous; tepals 4, minute; style central and deeply 2-lobed. Fruit a small fleshy 1-seeded drupe.

About 6 species ranging from southern Mexico to the Amazon basin, and in the Antilles. *Trophis chorizantha* Standl., with less congested staminate spikes and racemose pistillate inflorescences is to be expected in western Panama.

1. TROPHIS RACEMOSA (L.) Urb. Symb. Ant. 4:195. 1905.

Bucephalon racemosum L. Sp. Pl. 1190. 1753.
Trophis americana L. Syst. Nat. ed. 10. 1289. 1759.
Trophis americana β ramon Bur. et *γ meridionalis* Bur. in DC. Prodr. 17:253. 1873.
Sahagunia urophylla Donn. Sm. in Bot Gaz. 40:11. 1905.

Trees to about 15 m. in height. Leafy twigs rather slender, somewhat flexuose, glabrous, developing a yellowish gray bark. Leaves alternate, distichous, petiolate, the blade broadly oval to elliptic-oblong, occasionally irregularly pandurate, the tip subcaudate-acuminate, the base essentially equilateral and rounded to broadly obtuse, entire or somewhat serrate-undulate toward the tip, 6–20 cm. long, 2–9 cm. broad, firmly membranaceous, glabrous, the petiole 5–7 mm. long; stipules lateral, narrowly lanceolate, about 5 mm. long. Staminate spikes slender, 3–5 cm. long, bearing innumerable densely congested flowers interspersed with minute shortly stipitate peltate bracts: tepals 4, somewhat united at the base, broadly oval, about 2 mm. long, minutely papillate; stamens 4, the filaments about 3 mm. long, the anthers about 0.5 mm. long. Pistillate spikes rather short and strongly secund, 1.0–1.5 cm. long, densely and minutely ferruginous-puberulent, bearing rather few and distant sessile truncate conic flowers about 2 mm. long: perianth lobes minutely trigonal; stigma lobes about 1.5 mm. long. Fruits globose or ovoid, up to about 1 cm. long, reddish or yellowish, minutely puberulent.

Southern Mexico to the Amazon basin. *Ojoche macho, lechosa, ramón, gallote, morillo*; breadnut.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater, 4, 4a, Seibert 1581, 1583*; Almirante, *Cooper 349*; Old Bank Island, *Von Wedel 2075*; Water Valley, *Von Wedel 1599*; Río Cricamola between Finca St. Louis and Konkintoë, *Woodson, Allen & Seibert 1924*. CANAL ZONE: Barro Colorado Island, *Standley 41080, 41082*; Culebra, *Pittier 2255, 3627*; between France Field and Catival, *Standley 30296, 30235*; Gamboa, *Pittier 6636, 6637, 6652*; Río Pedro Miguel, near East Paraíso, *Standley 29963*; Gatún, *Standley 27287*; Fort Sherman, *Standley 30970*. CHIRIQUÍ: San Bartolomé, *Woodson & Schery 866*.

Fig. 37. *Trophis racemosa*

3. SOROCEA A. St.-Hil.

By WILLIAM C. BURGER

SOROCEA A. St.-Hil. in Mem. Mus. Paris 7:473. 1821.

Pseudosorocea Baill. in Adansonia 11:296. 1875.
Balanostreblus Kurz, emend. Hutchinson, in Kew Bull. 1918:152. 1918.

Dioecious trees, the branches unarmed. Leaves alternate, distichous; stipules lateral. Both staminate and pistillate inflorescences racemes and spikes; the small, congested or relatively distant flowers interspersed with small, shortly stipitate, peltate bracts. Staminate flowers: tepals 4, united or essentially free to the base, imbricate in bud, without an obvious pistillode; stamens 4, the filaments about as long as the tepals and scarcely inflexed before anthesis, the anthers broadly oval, extrorse. Pistillate flowers hypogynous to perigynous: tepals 4, completely united or minutely 4-lobed; ovary superior to inferior, the style central and deeply bifid. Fruit a small 1-seeded drupe.

About a dozen species ranging from Costa Rica to Argentina.

a. Leaves glabrous beneath, narrowly elliptic to elliptic-obovate, rarely over 20 cm. long, on narrow petioles 0.5–1.5 mm. thick; staminate flowers usually pedicellate. .... 1. S. AFFINIS
aa. Leaves generally short-pilose on the veins beneath, broadly elliptic to elliptic-oblong, to 30 cm. long, on petioles 1.5–2.5 mm. thick; staminate flowers sessile. .... 2. S. PUBIVENA

1. SOROCEA AFFINIS Hemsl. Biol. Centr.-Amer. Bot. 3:150. 1883.

Trees to about 15 m. Leafy twigs rather slender, slightly flexuose, glabrous, developing a yellowish gray bark. Leaves alternate, distichous, petiolate, the blades narrowly elliptic to elliptic-obovate, abruptly subcaudate-acuminate, the base equilateral and acutely cuneate, more or less serrate-undulate toward the tip, 6–20 cm. long, 2–8 cm. broad, firmly membranaceous, glabrous, the petiole about 2–10 mm. long; stipules narrowly lanceolate, about 5 mm. long. Staminate racemes 2–8 cm. long, bearing numerous rather closely spaced flowers interspersed with minute peltate bracts, minutely puberulent-papillate: tepals 4, somewhat united at the base, broadly oval, about 2 mm. long. Pistillate raceme rather short, 1–3 cm. long, elongating in fruit, minutely puberulent-papillate, bearing 8 or more shortly pedicellate flowers about 2 mm. long, the perianth thickened above the middle of the flower. Drupes subglobose, about 8 mm. broad, green with orange tip or bright red when fully mature.

Presently known only from lowland forests of Panama but probably extending south into Colombia.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *Von Wedel 1103, 1390*; Water Valley, *Von Wedel 598A, 961, 1715*; Almirante, *Cooper 554*. CANAL ZONE: Quebrada Melgada, *Steyermark 17494*; Gatún, *Johnston 1582, 1693*; Gamboa, *Standley 28412*; Las Cruces, *Seibert 576*; Barro Colorado Island, *Aviles 26, 52, 84, Seibert 566, Bailey & Bailey 538, Starry 314, Woodworth & Vestal 323, Bangham 558, 479, Salvoza 966, Standley 40797, 41053*; Trinidad River, *Pittier 4034*. CHIRIQUÍ: El Boquete, *Pittier 3045*. COCLÉ: El Valle, *Seibert 464*. COLÓN: Fató (Nombre de Dios), *Pittier 3856*; Palenque, *Pittier 4123*. DARIÉN: Ensenada Guayabo, *Stern & Chambers 180*. PANAMÁ: Arraiján, *Woodson, Allen & Seibert 1383*; Taboga Island, *Hayes 658*.

Fig. 38. *Sorocea affinis*

2. Sorocea pubivena Hemsl. Biol. Centr.-Amer. Bot. 3:150. 1883.

Trophis macrostachya Donn. Sm. in Bot. Gaz. 40:10. 1905.
Clarisia mollis Standl. in Ann. Missouri Bot. Gard. 30:85. 1943.

Trees to about 20 m. Leafy twigs rather thick (2–4 mm.), short-pubescent becoming glabrescent. Leaves alternate, distichous, petiolate, the blade broadly elliptic to elliptic-oblong, caudate-acuminate, the base equilateral and obtusely cuneate, entire to serrate-undulate, 10–30 cm. long, 5–10 cm. broad, firmly membranaceous, shortly pubescent beneath, the petiole about 8–20 mm. long; stipules narrowly acute, 6–8 mm. long. Staminate spikes 5–12 cm. long bearing numerous sessile flowers interspersed with minute peltate bracts; tepals 4, somewhat united at the base, about 2 mm. long, filaments broad and slightly connate at their base. Pistillate racemes short, elongating in fruit to 14 cm. bearing numerous flowers about 2 mm. long, the perianth thickened above, adnate to the ovary for about half its length. Drupes subglobose to ovoid, about 10 mm. broad.

Costa Rica to Panama.

bocas del toro: vicinity of Chiriquí Lagoon, *Von Wedel 1090* (Type of *Clarisia mollis* Standl.); Almirante, *Cooper & Slater 28*. chiriquí: Progreso, *Cooper & Slater 174*; vicinity of Gualaca, *Allen 5059*.

4. CLARISIA R. & P.

CLARISIA R. & P. Prodr. Fl. Peruv. & Chil. 128. 1794.

Sahagunia Liebm. in Kon. Danske Vidensk. Selsk. 2:316. 1851.
Soaresia Fr. Allem. in Arch. Palestr. Scientif. Rio Jan. 1:142. 1858.
Acanthinophyllum Fr. Allem. in Rev. Brazil. 1:368. 1858.

Dioecious trees, the branches unarmed. Leaves alternate, distichous; stipules lateral. Both staminate and pistillate inflorescences secund racemes and spikes, or the pistillate subcapitate or in some species reduced to paired or solitary axillary flowers, bearing small, shortly stipitate, peltate bracts as in *Trophis* and *Sorocea.* Staminate flowers with a single stamen and an indefinite vestigial perianth, the anther broadly oval. Pistillate flowers epigynous, with 4 minute superior perianth lobes and an inconspicuous but persistent basal involucre of several peltate bracteoles, the style central and deeply 2-lobed. Fruit a small 1-seeded drupe.

About 8 species ranging from southern Mexico to Brazil and Peru according to Lanjouw (in Rec. Trav. Bot. Néerl. 33:254. 1936.).

Fig. 39. *Clarisia panamensis*

1. CLARISIA **panamensis** Woodson, spec. nov.

Arbores usque ca. 10 m. altitudine attigentes ramulis sat validis glabris maturitate cortice tenue brunneo-griseo tectis. Folia alternata disticha lamina late obovato-elliptica apice obtuse subcaudato-acuminata basi obtusa 10–15 cm. longa 5–7 cm. lata membranacea glabra margine integra venis utroque latere ca. 10–12 petiolo valido ca. 1 cm. longo; stipulis lateralibus anguste lanceolatis ca. 1 cm. longis. Inflorescentiae femineae racemosae usque ca. 6-florae rhachide in fructu ca. 2 cm. longo glabro floribus ignotis. Inflorescentiae ac flores masculae ignotae. Fructus brevissime pedicellati late obovoideo-ellipsoidei ante maturitate usque 2.5 cm. longi 1 cm. crassi apice styli lobis persistentibus linearibus recurvatis ornati basi bracteis involucratis peltatis pluribus minutissime puberulis cincti.

COCLÉ: region north of El Valle de Antón, alt. 1000 m., September 27, 1946, *P. H. Allen 3741* (MO, HOLOTYPE).

This species keys to the general relationship of *C. colombiana* (Rusby) Lanj. in Lanjouw's treatment. The latter is known only from a single staminate specimen

Fig. 40. *Clarisia mexicana*

(*H. H. Smith 424*) which has smaller, narrowly obovate, strikingly caudate leaves. The fruits of *C. panamensis* differ both in shape and in size from those of any other *Clarisia* presently known.

Also to be expected in western Panama is *C. mexicana* (Liebm.) Lanj., which is known from the Golfo Dulce region of Costa Rica. It may be distinguished readily from *C. panamensis* by its rather narrowly oblong leaves and small globose fruits.

5. BROSIMUM Sw.

Brosimum Sw. Prodr. Veg. Ind. Occ. 12. 1788, nom. conserv.

Alicastrum P. Br. Hist. Jam. 372. 1756, nom. rejic.
Piratinera Aubl. Hist. Pl. Guian. Fr. 2:888. 1775, nom. rejic.
Galactodendrum Humb. Relat. Hist. 2:108. 1819.
Brosimopsis S. Moore, in Trans. Linn. Soc. 2 ser. 4:473. 1895.

Monoecious or perhaps occasionally dioecious trees. Leaves alternate, distichous; stipules lateral to fully amplexicaul. Inflorescences globular to turbinate,

typically monoecious with 1–2 central pistillate flowers surrounded by numerous minute staminate commingled with more or less conspicuous peltate bracts, but infrequently dioecious. Pistillate flowers: epigynous, the perianth vestigial, the stigma deeply 2-lobed and apparently proterogynous. Staminate flowers with a definite 4-lobed perianth or the perianth vestigial or lacking; stamens 4, 2 or 1, the anthers oblongoid and basifixed to circular and peltate, dehiscing longitudinally to circumscissilly. Fruit a false drupe.

Probably about 24 species ranging from southern Mexico to Argentina, and in the Antilles. A genus most interesting in its floral modifications and very badly in need of revision, as are most Moraceae.

The first three species of the enumeration which follows would be referable to *Brosimopsis* if a narrow generic concept were followed consistently in this treatment. I have indicated in a previous paragraph that I am not in sympathy with such a view and follow it in other instances merely in deference to previously established custom. In this case, however, custom is not greatly involved. Amongst the Panamanian genera of Moraceae alone no less than four parallel reductions of the male flowers to a vestigial perianth and a single stamen may be observed: *Trophis* → (*Sorocea*) → *Clarisia*; *Brosimopsis* → *Brosimum*; *Perebea* → *Castilla*; *Olmedia* → *Pseudolmedia*.

The eight Panamanian species also show a most interesting transition in the structure of the anther from a rather commonplace basifixed type with longitudinal dehiscence to a most unusual peltate body with perfectly symmetrical circumscissile dehiscence, aptly described by Aublet (loc. cit. sub *Piratinera*) as "*en forme de champignons*". The series is illustrated in the accompanying figures.

In the following text two new Costa Rican species are described, since they have been collected only a few miles from the Panamanian border and probably will yet be discovered in our flora.

a. Flowers not wholly concealed before anthesis by the weakly expanded, long-stipitate peltate bracts, with a conspicuous perianth and 2–4 stamens with oblongoid basifixed anthers; heads globose; stipules lateral, their scars about half-surrounding the stem (except *B. allenii*).
  b. Stipules lateral; leaves membranaceous, oblong to obovate-oblong; flowering peduncles slender, almost as long as the rather small and delicate heads or somewhat longer; flowers with essentially equal tepals and 2–4 stamens.
    c. Leaves relatively large, 2- to 3-times as long as broad, glabrous; anthers setose-appendiculate; fruits relatively large, the seed about 2 cm. long .... 1. B. OJOCHE
    cc. Leaves relatively small, 3- to 4-times as long as broad, softly white-tomentellous beneath; anthers exappendiculate; fruits relatively small, the seed about 1 cm. long .... 2. B. COSTARICANUM
  bb. Stipules almost fully amplexicaul, their scars almost completely surrounding the stem; leaves rather heavily coriaceous, ovate-elliptic; flowering peduncles stout, much shorter than the massive heads; flowers with strongly unequal tepals and 2 stamens .... 3. B. ALLENII
aa. Flowers wholly concealed before anthesis by the strongly expanded, shortly stipitate peltate bracts, with a vestigial or obsolete perianth and 1 stamen with a nearly circular anther; stipules almost fully amplexicaul, their scars nearly surrounding the stem (except *B. guianense*).
  b. Stipules lateral, about 3–5 mm. long; heads obconic or turbinate .... 4. B. GUIANENSE
  bb. Stipules almost fully amplexicaul; heads globose.

c. Stipules 1.5–3.0 cm. long; flowering peduncles stout; anthers obliquely inserted on the filament, clearly longitudinal in dehiscence. .... 5. B. UTILE
cc. Stipules 5–10 mm. long; flowering peduncles slender; anthers peltately inserted on the filament, circumscissile in dehiscence or falsely so.
d. Anthers excentrically peltate, dehiscing by 2 basal valves; leaves elliptic-obovate. .... 6. B. BERNADETTEAE
dd. Anthers centrally peltate, dehiscing circumscissilly.
e. Leaves oval to oblong-elliptic, obtuse to shortly subcuspidate-acuminate; peduncles about as long as the flowering heads to somewhat shorter. .... 7. B. ALICASTRUM
ee. Leaves broadly ovate to oblong-ovate, narrowly subcaudate-acuminate; peduncles much longer than the flowering heads. 8. B. TERRABANUM

1. BROSIMUM **ojoche** Woodson, spec. nov.

Arbores magnae usque 35 m. altae ut dicitur, ramulis sat tenuibus glabris. Foliorum lamina oblonga vel obovato-oblonga apice obtuse acuminata basi late obtusa ca. 9–18 cm. longa 4–7 cm. lata firme membranacea glabra, petiolo 5–15 mm. longo; stipulis lateralibus ovato-lanceolatis 5–7 mm. longis cicatrice ramulum ca. dimidia cingenti. Inflorescentiae capituli usque 5–7 mm. pedunculati globosi ca. 1 cm. diametro metientes nostri prosus masculi an semper dioeci; florum masculorum tepalis 4 subliberis aequalibus ca. 1.5 mm. longis, staminibus 4 valde exsertis antheris oblongoideis apice setoso-appendiculatis basifixis longitudinaliter dehiscentibus ca. 1 mm. longis. Flores feminei ignoti. Fructus globosi ultra 2.5 cm. diam. metientes semine ca. 2 cm. longo.

Fig. 41. *Brosimum ojoche*

COSTA RICA: CARTAGO: forêts de Turrialba, alt. 570 m., *Tonduz 8338* (US); pâturages de Turrialba, alt. 650 m., *Nuñez 16353* (US); PUNTARENAS: Esquinas forest, region between Río Esquinas and Palmar Sur de Osa, alt. 75 m., Jan. 30, 1951, *P. H. Allen 5809* (US, HOLOTYPE); Hacienda Liscano, vallée du Barú, alt. 0 m., *Pittier 12082* (US).

A northern extension of *B. ojoche* may be represented by five specimens from British Honduras which are discussed briefly under *B. terrabanum*.

This species and two which follow, although at present known only from Costa Rica, have been collected so close to the Panamanian border that it seems quite likely that sooner or later they will be found in Panama. The Allen specimen was identified previously as *B. terrabanum* Pittier, while the Nuñez and Brenes specimens were determined as *B. costaricanum* Liebm. by Pittier, who himself included his own collection within *Helicostylis montana* Pittier which, as it happens, is synonymous with true *Brosimum costaricanum*. It is curious that Pittier, although particularly interested in *Brosimum*, twice described species of that genus as species of *Helicostylis*, a genus which has yet to make its appearance in Central America as far as I am aware.

Brosimum ojoche, the specific epithet of which is taken from the vernacular name noted upon three of the cited sheets, is easily distinguished from *B. costaricanum* by the characters of the key. It appears more than somewhat questionable to me that the specimens from Cartago and those from Puntarenas could reasonably represent a single species but the foliage of the four sheets is strikingly similar. The Allen specimen is in flower while the three others are in fruit (in a rather pitiful state of disintegration).

2. BROSIMUM COSTARICANUM Liebm. in K. Dansk. Vidensk. Selsk. Skr. ser. 5. 2:334. 1851.

Helicostylis montana Pittier, in Contrib. U. S. Nat. Herb. 20:96. 1918.
Brosimum sapiifolium Standl. & L. Wms. in Ceiba 3:40. 1952.

Trees up to 30 m. tall, the younger twigs relatively slender, softly white-puberulent to glabrate. Leaves relatively small, rather narrowly obovate-oblong, the tip rather abruptly subcaudate-acuminate, the base obtuse or rounded, 8–18 cm. long, 2–4 cm. broad, membranaceous, softly white-tomentellous or puberulent on the veins beneath; petioles about 5 mm. long. Inflorescences possibly dioecious, globose, the staminate with peduncles about 1 cm. long, very slender, about 1 cm. in diameter. Staminate flowers: tepals 5, nearly free and essentially equal, about 2 mm. long; stamens 3–4, widely exserted, the anthers basifixed, oblongoid, about 1 mm. long. Pistillate flowers presently unknown. Nearly mature fruits globose, about 1.5 cm. in diameter, with persistent peltate bracts, the seed about 1 cm. long.

Costa Rica and Panama, in lowland forests.

CHIRIQUÍ: Paso de Quebrada Gato, between Hato Jobo and San Félix, *Pittier 5426*; Progreso, *Cooper & Slater 188*.

Brosimum ramonense Standl. of eastern Costa Rica, which may be expected in western Panama, differs from *B. costaricanum* chiefly in the scant and appressed ferruginous pubescence of the leaves.

Fig. 42. *Brosimum costaricanum*

3. Brosimum **allenii** Woodson, spec. nov.

Arbores magnae ut dicitur usque ca. 40 m. altitudine attingentes vulgo *palo de vaca* incolarum appelatur quod latice potabili, ramulis crassiusculis internodiis congestis glabris. Folia late ovato-elliptica abrupte brevissime acuminata basi rotunda 9–20 cm. longa 5–12 cm. lata coriacea omnino glabra, petiolis crassis ca. 1.5 cm. longis; stipulis amplexicaulibus ovatis longe acuminatis ca. 1.5 cm. longis cicatrice ramulum transverse cingenti. Inflorescentiae globosi ca. 1.5 cm. diam. metientes nostri monoici flore unico feminei cum masculis floribus multis, pedunculo crasso perbrevi ca. 8 mm. longo; florum masculorum tepalis 5 inaequalibus ca. 1 mm. longis, staminibus 2 valde exsertis antheris oblongoideis basifixis longitudinaliter dehiscentibus ca. 1 mm. longis. Fructus non visi.

Costa Rica: puntarenas: Esquinas forest, region between Río Esquinas and Palmar Sur de Osa, alt. 75 m., Jan. 30, 1951, *P. H. Allen 5813* (US, holotype).

Mr. Allen reports that the latex of this species, which he associated with *B. utile*, the famous "cow tree" first discovered by von Humboldt, is "of good flavor, rather like condensed milk, good in coffee." I believe that *B. allenii* is sufficiently distinguishable from true *B. utile* through the characters of the preceding key.

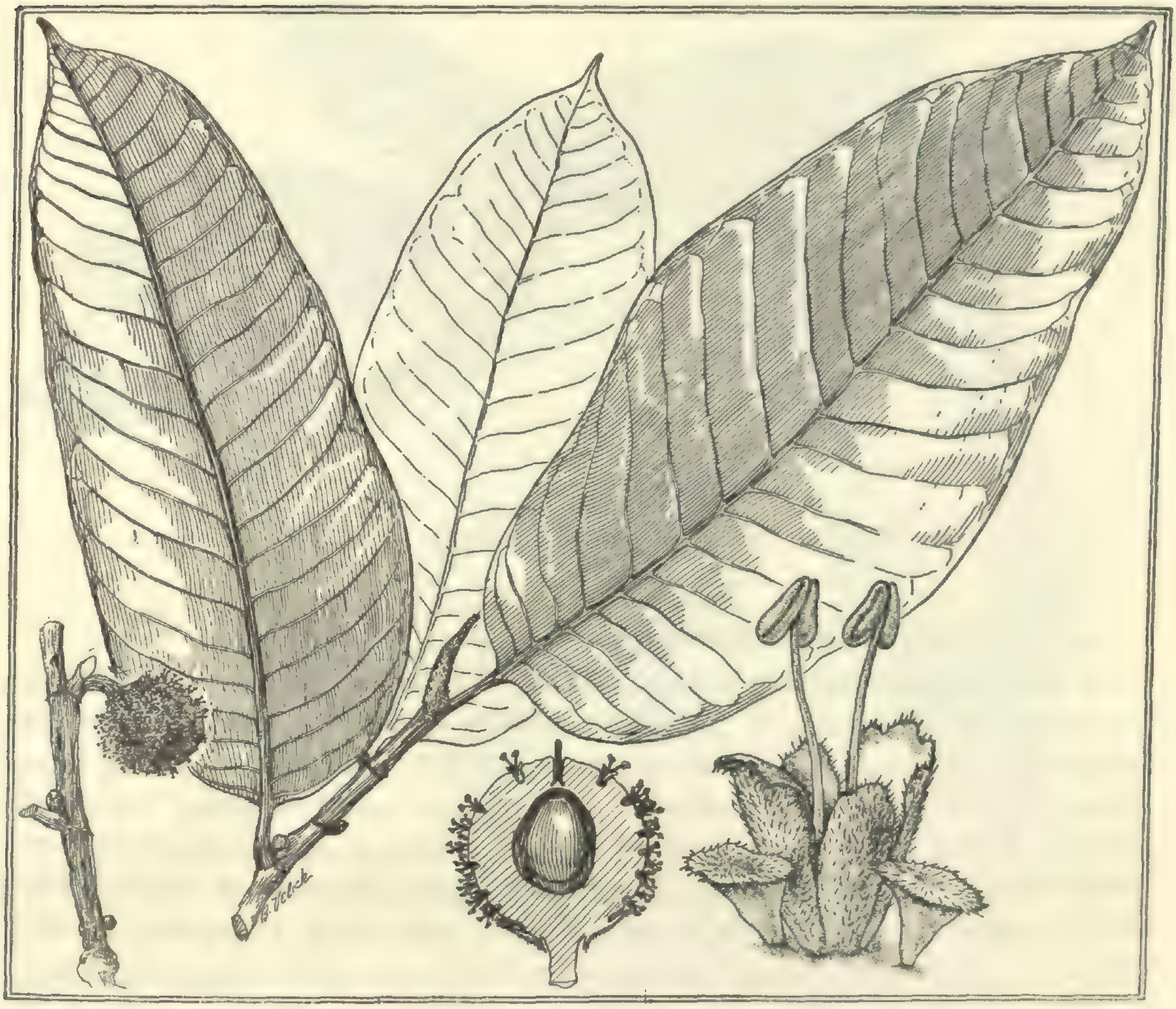

Fig. 43. *Brosimum allenii*

4. Brosimum guianense (Aubl.) Huber, in Bull. Mus. Goeldi 5:337. 1909.

Piratinera guianense Aubl. Hist. Pl. Guian. Fr. 2:888; 4: *t. 340*. 1775.
Piratinera panamensis Pittier, in Contrib. U. S. Nat. Herb. 20:100. *pl. 7*. 1917.
Brosimum panamense (Pittier) Standl. & Steyerm. in Field Mus. Publ. Bot. 23:40. 1944.

Trees to about 25 m. tall, essentially glabrous throughout. Leaves oblong-obovate, abruptly and obtusely acuminate to subcuspidate, the base broadly obtuse to rounded, entire, 5–12 cm. long, 2.5–4.0 cm. broad, firmly membranaceous, the petiole about 5 mm. long; stipules lateral, about 5 mm. long. Heads broadly obconic to turbinate, usually somewhat lobed or convolute, about 7–10 mm. broad, the slender peduncle about 1.0–1.5 cm. long. Staminate flowers with a low vestigial perianth and 1 stamen with a rather thick filament about 2 mm. long and an obliquely inserted broadly oval anther up to 1 mm. long, associated with suborbicular shortly-stipitate peltate bracts. Pistillate flowers 1–3. Mature fruit unknown.

British Honduras to Venezuela, in lowland forests.

Fig. 44. *Brosimum guianense*

SAN BLAS: Puerto Obaldía, *Pittier 4336.*

A photograph of Aublet's collection at the British Museum shows that Pittier was correct in associating *P. panamensis* with *P. guianensis*; they probably are conspecific. *Pittier 4336* is represented in the U. S. National Herbarium by three sheets, each with several inflorescences. I have been unable to detect the plural pistillate flowers which Pittier considered so important in maintaining *Piratinera* distinct from *Brosimum*, either in the remnants of the inflorescences which Pittier himself supposedly dissected or in an additional one which I dissected myself. One head, however, does indeed appear to be pistillate (without external evidence of staminate flowers), but I have not had the temerity to dissect it. Here, as in other species of *Brosimum* in Panama, the heads would appear frequently to be unisexual. As Standley expresses it pointedly in the cited references, "In typical *Brosimum* there is only one pistillate flower, in *Piratinera* two; but with ordinary herbarium specimens it is difficult to find even one pistillate flower, to say nothing of discovering two, and the difference is at least not a practical one."

5. BROSIMUM UTILE (HBK.) Pittier, in Contrib. U. S. Nat. Herb. 20:102. 1918.

Galactodendrum utile HBK. Nov. Gen. & Sp. 7:163. 1825.
Brosimum galactodendron D. Don, in Sweet, Hort. Brit. ed. 2. 462. 1830.

Trees 20–25 m. in height, with young twigs rather stout and with rather close internodes, minutely and indefinitely puberulent when young, eventually developing a rather thick periderm. Leaves rather broadly oblong, abruptly and acutely acuminate, rounded at the base, 10–25 cm. long, 3–10 cm. broad, subcoriaceous, sparsely puberulent to glabrate, the petioles stout, 5–15 mm. long; stipules amplexicaul, lanceolate, long-acuminate, 2–3 cm. long, pilosulose, leaving oblique scars nearly encircling the stem. Inflorescences globose, monoecious, about 1 cm. in diameter, the peduncle of about equal length, rather stout, staminate flowers: without an obvious perianth and with a single stamen with a broadly oval anther

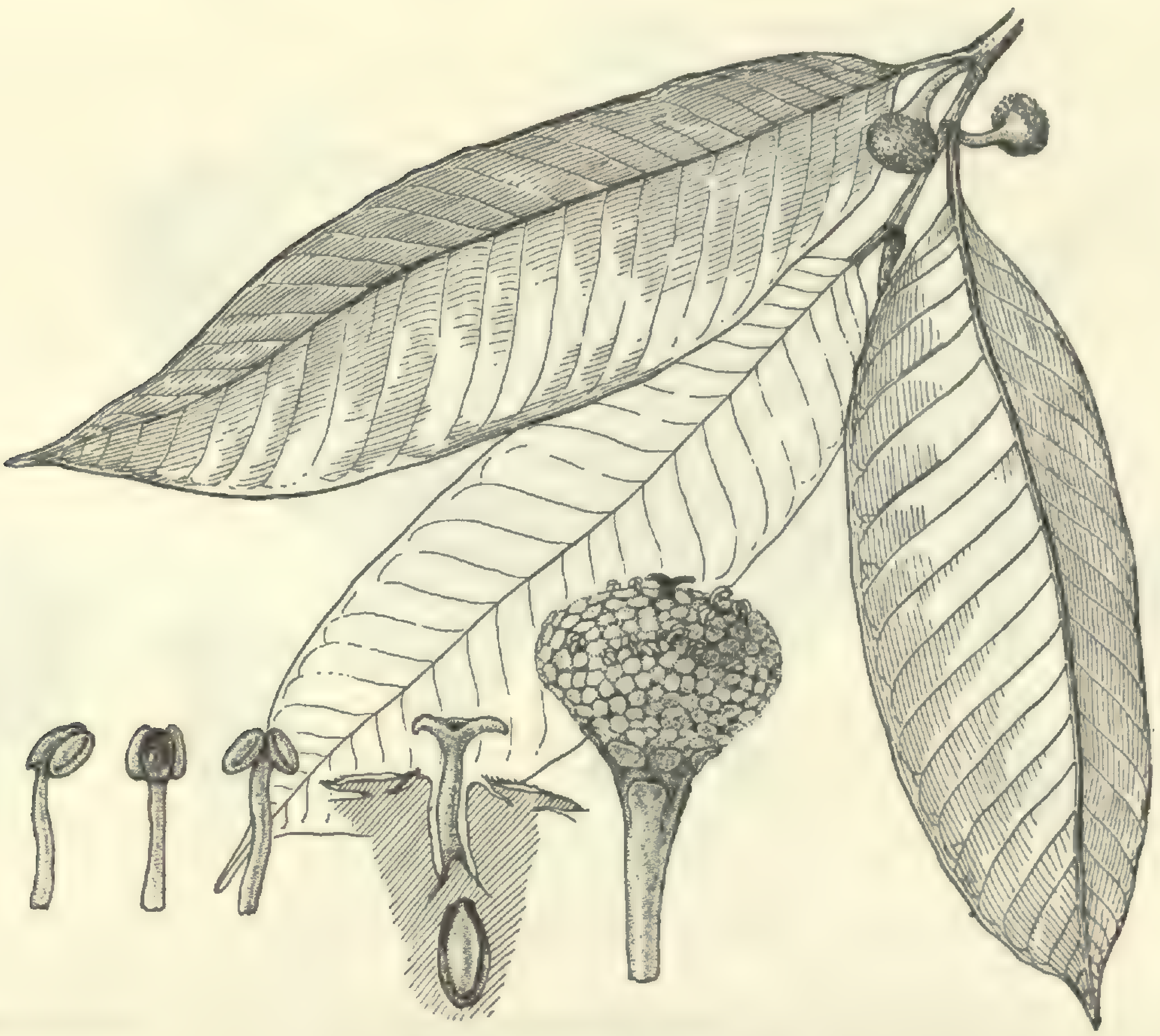

Fig. 45. *Brosimum utile*

obliquely affixed to the filament, obviously longitudinal in dehiscence. Fruit depressed-globose, 2.0–2.5 cm. in diameter.

Costa Rica to Colombia.

SAN BLAS: hills of Sperdí, near Puerto Obaldía, *Pittier 4345, 4418.*

This is von Humboldt's "cow tree" (*palo de vaca*) with potable latex.

6. BROSIMUM **bernadetteae** Woodson, nom. nov.

Helicostylis latifolia Pittier, in Contrib. U. S. Nat. Herb. 20:95. 1914, non *Brosimum latifolium* Standl. in Trop. Woods 42:26. 1935.

Trees to about 25 m. tall, the branches grayish brown, inconspicuously puberulent to glabrate. Leaves elliptic-obovate, broadly acuminate-subcuspidate to obtuse or rounded at the tip, broadly cuneate to rounded at the base, 6–12 cm. long, 3–6 cm. broad, with about 12–18 pairs of rather crowded veins, subcoriaceous, glabrous, the petioles about 4–7 mm. long; stipules almost fully amplexicaul, about 5–7 mm. long. Inflorescences subglobose, ours staminate, about 5 mm. in diameter at anthesis, the peduncle about 4–5 mm. long. Staminate flowers without an obvious perianth; stamen 1, the anther excentrically peltate, about 1 mm. in diameter, dehiscing by 2 basal valves. Pistillate flowers and fruit unknown.

Panama, in lowland forests.

Fig. 46. *Brosimum bernadetteae*

CANAL ZONE: Barro Colorado Island, *Standley 41156, Kenoyer 662.* DARIÉN: Yaviza, *Pittier 6584.* PANAMÁ: Alhajuela, Chagres Valley, *Pittier* 3488.

This species so closely resembles *B. alicastrum* that the slight but very significant difference in the structure on the anthers had escaped me until it was called to my attention by our artist for the FLORA OF PANAMA, Mrs. Bernadette Velick. Nevertheless, the difference also apparently was noticed by Pittier and its significance over-emphasized as the synonymy testifies. Mrs. Velick was unable to detect the perianth segments described by Pittier, nor could I.

After an examination of the type specimen of *B. latifolium* Standl. (*Eggers 15721*, F), which bears a single immature pistillate head, I have concluded that it should be referred to *B. alicastrum* Sw.

7. BROSIMUM ALICASTRUM Sw. Prodr. Veg. Ind. Occ. 12. 1788.

Brosimum latifolium Standl. in Trop. Woods 42:26. 1935.

Trees to about 30 m. tall, the young branches slender, grayish brown, glabrous or essentially so. Leaves oval to oblong-elliptic, obtuse to shortly subcuspidate-acuminate at the tip, broadly obtuse to rounded at the base, 5–15 cm. long, 2–6 cm. broad, with about 12–18 pairs of slender veins, firmly membranaceous, glabrous, the petioles about 5–7 mm. long; stipules almost fully amplexicaul, about 5 mm. long. Inflorescences subglobose, monoecious or dioecious, 3–6 mm. in diameter at anthesis, the peduncle slender, about as long as the heads or somewhat shorter. Staminate flowers with a very indefinite vestigial perianth; stamen 1, the anther circular,

Fig. 47. *Brosimum alicastrum*

centrally peltate and dehiscing circumscissilly, about 1 mm. in diameter. Fruit about 1.5 cm. in diameter.

Southern Mexico to Ecuador; Cuba and Jamaica, at low elevations.

CHIRIQUÍ: Progreso, *Cooper & Slater 239, 263.*

Brosimum bernadetteae, B. alicastrum and *B. terrabanum* appear to be well founded upon the basis of flower and inflorescence structure, but the leaves are not particularly distinctive. At the present time it is difficult to define their natural ranges not only because of the rather few fertile specimens available in herbaria but also because of the large number of sterile specimens labeled either as *B. alicastrum* or *B. terrabanum* which add considerable confusion and would much better have been left upon the trees.

8. BROSIMUM TERRABANUM Pittier, in Contrib. U. S. Nat. Herb. 18:69. 1914.

Piratinera terrabana (Pittier) Lundell, in Carnegie Inst. Wash. Publ. 478:208. 1937, as to basinym, not as to specimens cited.

Trees up to about 25 m. tall, the young branches moderately stout, reddish brown, indefinitely pilosulose to glabrate. Leaves broadly ovate to oblong-ovate, narrowly subcaudate-acuminate at the tip, broadly obtuse to rounded at the base, 10–25 cm. long, 3–9 cm. broad, with 18–22 pairs of prominent veins, subcoriaceous, glabrous, the petioles quite stout, about 1 cm. long; stipules almost fully amplexicaul, about 1 cm. long, minutely pilosulose. Flowering heads apparently usually dioecious, subglobose, 4–6 mm. in diameter at anthesis, the peduncles very slender, two or three times longer than the heads. Staminate flowers with an indefinite vestigial perianth; stamen 1, the anther circular, centrally peltate, about 1 mm. in diameter, dehiscing circumscissilly. Fruit unknown.

Costa Rica and Panama (doubtfully in Guatemala and El Salvador), in lowland forests.

BOCAS DEL TORO: Farm 8, region of Almirante, *Cooper 441*.

Lundell misapplied *B. terrabanum* to include two specimens from British Honduras, *Gentle 1737* and *Schipp 522*, which, together with three others of the same collectors deposited in the herbarium of the Missouri Botanical Garden (*Schipp 1360*; *Gentle 3307, 3440*) appear to me probably to represent a northern extension of *B. ojoche*.

6. BATOCARPUS Karst.

BATOCARPUS Karst. Fl. Colomb. 2:67, 1863, emend. Woodson, non sensu Fosberg in Proc. Biol. Soc. Wash. 55:101. 1942.

Dioecious trees. Leaves alternate, distichous; stipules lateral. Staminate inflorescences in discoid involucrate heads, the bracts and bracteoles basifixed, not peltate. Pistillate inflorescences in globose heads without involucral bracts nor obvious bracteoles. Staminate flowers with a deeply 4-lobed perianth and 4 stamens with broadly oval longitudinally dehiscent anthers apically attached to the filaments. Pistillate flowers with a fleshy tubular accrescent perianth, the ovary superior and with a central deeply 2-lobed papillate stigma. Fruit a globose rather fleshy syncarp.

Two well-authenticated species, the following and *B. costaricensis* Standl. and L. Wms., which may be expected in western Panama.

1. BATOCARPUS ORINOCENSIS Karst. Fl. Colomb. 2:67. *pl. 134*. 1863.

Trees to about 10 m. in height, the young twigs slender, minutely puberulent when very immature, becoming glabrate. Leaves broadly elliptic to oval-obovate, rather abruptly subcaudate-acuminate, broadly obtuse to rounded at the base, 8–20 cm. long, 4–7 cm. broad, entire, membranaceous, glabrous, the petiole slender, about 1 cm. long; stipules about 5 mm. long, narrowly lanceolate. Staminate heads discoid, about 1 cm. in diameter, prominently involucrate with several broadly ovate minutely tomentellous bracts about 2 mm. long, the peduncle about 8 mm. long. Pistillate heads globose, about 2 cm. in diameter, the peduncle about 1 cm. long, without a definite involucre.

Panama to Amazonian Colombia and Peru.

BOCAS DEL TORO: Buena Vista Camp on Chiriquí Trail at 1250 ft., *Cooper 601*.

The staminate heads of this specimen (US) indeed superficially resemble those of *Brosimum costaricanum* Liebm. as originally identified, but dissection discloses the absence of the peltate bracteoles essential to *Brosimum*. The shape and size of the leaves and the character of the stipules agree startlingly with the excellent plate of a pistillate specimen of *Batocarpus orinocensis* provided by Karsten, and there appears to me no doubt concerning the identity of the two.

Fig. 48. *Batocarpus orinocensis*
(Pistillate details after Karsten)

If this be true, our specimen thus provides the first information concerning the staminate structures of the genus, known previously only from Karsten's plate and the citation of an additional pistillate specimen from Peru by Fosberg (loc cit. 1942), since the second species, *Batocarpus costaricensis* Standl. & L. Wms., also is known only from pistillate specimens.

This view is in conflict with that of Fosberg that *Batocarpus* and *Anonocarpus* Ducke, a monotypic genus, are congeneric. *Anonocarpus amazonicus* Ducke (in Archiv. Jard. Bot. Rio Jan. 3:39. 1922) fortunately was described with full details of both staminate and pistillate inflorescences, the former being elongate spikes of naked 1-staminate flowers. Since the pistillate inflorescences of *Batocarpus* and *Anonocarpus* have much in common, as noted by Ducke, it is easy to sympathize with Fosberg's impulse to merge the two. This now becomes less plausible since inflorescence structure is such an inflexible criterion of genera in Moraceae.

Batocarpus costaricensis, presently known from western Puntarenas Province, Costa Rica, and to be expected in western Panama, is well distinguished from *B. orinocensis* by the prominently repand-serrate leaves and nearly sessile pistillate heads.

7. PEREBEA Aubl.

Perebea Aubl. Hist. Pl. Guian. Fr. 2:952; 4: *t. 361.* 1775.

Mikania Neck. Elem. Bot. 2:217. 1790, non Willd.

Dioecious trees. Leaves alternate, distichous, entire to rather obscurely undulate-serrate toward the tip; stipules fully amplexicaul. Inflorescences axillary, solitary or clustered, involucrate, discoid. Staminate flowers: tepals 4, free or more or less united; stamens 4, nearly included, the anthers broadly oval. Pistillate flowers numerous and all fertile; tepals 4, free or somewhat united, accrescent and somewhat pulpy in fruit but essentially free and united only at the base; ovary superior to subinferior, the style central, the 2 stigma lobes short and broad to narrow and filiform. Fruit a more or less fleshy, weakly united syncarp.

Perhaps 4–6 species from Costa Rica to Brazil and Bolivia. Of the related South American genera may be mentioned *Helicostylis,* which differs from *Perebea* in the exinvolucrate inflorescences, the pistillate being most peculiar in having only one or very few of the epigynous central flowers fertile and the peripheral flowers reduced to a sort of enveloping involucre composed of the accrescent fleshy sterile perianths.

a. Leaves predominantly cordate or subcordate, the stipules 2–4 cm. long; pistillate heads with approximately 25–50 flowers, 5–6 cm. broad in fruit, the bracts acuminate .... 1. P. guianensis

aa. Leaves obtuse to rounded at the base, the stipules 5–10 mm. long; pistillate heads with about 5–10 flowers, 2–3 cm. broad in fruit, the bracts obtuse. .... 2. P. xanthochyma

Fig. 49. *Perebea guianensis*

1. Perebea guianensis Aubl. Hist. Pl. Guian. Fr. 2:952; 4: *t. 361.* 1775.

Perebea castilloides Pittier, in Contrib. U. S. Nat. Herb. 13:438. *t. 80-81.* 1912.
Perebea pseudopeltata Mildbr. in Notizbl. 10:184. 1927.
Perebea tessmannii Mildbr. loc. cit. 185. 1927.
Perebea laevigata Standl. in Trop. Woods 16:36. 1928, nom. nud. in syn.
Perebea glabrata Standl. in Field Mus. Publ. Bot. 4:201. 1929.
Perebea acanthogyne Ducke, loc. cit. 11:579. 1932.

Small trees infrequently to 20 m. tall, with rather stout flexuose ferruginous-hirsutulous branches. Leaves broadly oblong-elliptic grading toward obovate or ovate, the apex abruptly and narrowly subcaudate-acuminate, the base predominantly more or less deeply cordate, infrequently broadly obtuse or rounded in young leaves, entire to indefinitely undulate-serrate toward the tip, 15–40 cm. long, 7–15 cm. broad, firmly membranaceous, more or less ferruginous-hirtellous, particularly beneath, the petiole rather stout, 5–10 mm. long; stipules narrowly ovate-lanceolate, long-acuminate, 2–4 cm. long, densely sericeous. Staminate heads about 1.0–1.5 cm. in diameter, the peduncle about 1 cm. long. Pistillate heads superficially similar to the staminate with about 25–50 flowers. Fruiting heads oblate-ovoid, about 5–6 cm. broad, the achenes about 1 cm. long.

Panama to Brazil and Bolivia, in lowland forests. Reported as *cerillo* by Standley, *ule* and *cuacho* by Proctor Cooper.

BOCAS DEL TORO: Cricamola, *Cooper 523*; Punta Peña, near Chiriquí Grande, *Pittier s. n.* CANAL ZONE: west of Pina Base Camp, Limón Bay, *Johnston 1607*; Frijoles, *Standley 27453*. SAN BLAS: Permé, *Cooper 634*.

The association of these plants with Aublet's name is made with some misgivings. *Perebea guianensis* was excellently and unmistakably illustrated by Aublet, but it is doubtful whether the holotype exists at Paris, since Trécul apparently was not able to find it and my friend Dr. F. G. Meyer did not find an isotype at the British Museum. Dr. Meyer did find a staminate specimen, apparently of this species collected by Martin in 1804, a duplicate of which is now available not only at the British Museum (and presumably Paris?) but at the Missouri Botanical Garden. This sheet corresponds generally to those cited from Panama on the one hand and on the other to several collections from South America which, because they are now distributed under other names, I shall cite both in support of my interpretation and for the use of others: Brazil: *Krukoff 4827, 7041, 7209, 8076, 8350, Ducke 1221* (24-5-1940) Peru: *Klug 2719, R. C. Lorenz 3210*—all deposited in the herbarium of the Missouri Botanical Garden. For positive identification fruiting specimens from Panama are necessary, and I must confess that some of the Panamanian sheets are noticeably more pubescent than these from Brazil and Peru.

2. Perebea xanthochyma Karst. Fl. Colomb. 2:23. *t. 112.* 1862.

Perebea integrifolia Karst. loc. cit. 1862.
Castilloa markhamiana J. Collins, Rept. Caoutch. 12. *t. 3.* 1872.
Perebea markhamiana (J. Collins) Benth. ex Hook. f. in Trans. Linn. Soc. 2 ser. 2:211. 1886.
Perebea hispidula Standl. in Ann. Missouri Bot. Gard. 29:350. 1942.

Perebea molliflora Standl. & L. Wms. in Ceiba 3:41. 1952.
Perebea trophophylla Standl. & L. Wms. loc. cit. 196. 1953.

Small trees to about 10 m. tall, with rather slender and scarcely flexuose hispidulous to glabrate branches. Leaves oblong-elliptic, subcaudate, acuminate to abruptly subcuspidate at the tip, the base broadly obtuse to rounded, usually more or less conspicuously undulate-serrate toward the tip, infrequently subentire, 8–28 cm. long, 3–9 cm. broad, rather inconspicuously appressed-puberulent beneath to nearly glabrous, the petiole about 5 mm. long; stipules lanceolate, 5–10 mm. long. Staminate heads about 5 mm. in diameter, sessile or subsessile. Pistillate heads usually with about 5–10 flowers about 5 mm. in diameter, the peduncle rather slender, 3–5 mm. long, fruiting heads subsessile, about 1 cm. in diameter, the achenes to about 1 cm. long.

Costa Rica to Colombia, in lowland forests.

BOCAS DEL TORO: Daytonia Farm, *Cooper 425*; Old Bank Island, *Von Wedel 1935*. CANAL ZONE: Gatún, *Johnston 1692*.

These sheets agree very well with Karsten's plate which illustrates both *P. xanthochyma* and *P. integrifolia* (the chief differentium of which would appear to be sex!), and with a fragment of Karsten's isotype of the former (F).

8. CASTILLA Cerv.

CASTILLA Cerv. in Gac. Lit. Mexico, Suppl. 7. 1794.

Castilloa auct.

Monoecious or dioecious trees (cf. O. F. Cook, in Science, ser. 2. 18:437. 1903; H. Pittier, in Contrib. U. S. Nat. Herb. 13:253. 1910), the branches unarmed. Leaves alternate, distichous, closely and minutely ciliate-denticulate to essentially entire; stipules fully amplexicaul. Inflorescences axillary, solitary or clustered, involucrate, the staminate discoid and conduplicate-flabellate, the pistillate discoid or subglobose. Staminate flowers essentially unorganized and naked, with stamens bearing oval anthers apically affixed to the filament. Pistillate flowers more or less coherent, with a fleshy accrescent conic-tubular perianth and a subinferior ovary, the stigma 2-lobed almost to the base of the central style. Fruit a more or less fleshy syncarp.

Probably no more than 4–6 species extending from southern Mexico to Bolivia. Pittier (loc. cit. 1910) provides a very difficult key to 10 species which I have found to be quite impractical when applied to herbarium specimens; I suspect that it would also present problems in the field. From the evidence available to me, I can visualize at most two scarcely distinguishable species in Panama. The genus has been of sporadic interest in the past as a possible source of commercial rubber.

a. Leaves more or less cordate and usually nearly equilateral at the base: pistillate flowers half or more coherent and developing an orange or reddish pulp in fruit.......... 1. C. ELASTICA

aa. Leaves obtuse to acute and very strongly inequilateral at the base; pistillate flowers coherent only at the very base, greenish and nearly dry in fruit.......... 2. C. TUNU

1. Castilla elastica Cerv. in Gac. Lit. Mexico, Suppl. 7. 1794.

Castilla panamensis Cook, in Science, n. ser. 18:438. 1903.

Trees 5–10 m. tall, the young branches densely hirsute with spreading (less frequently appressed) golden hairs, eventually glabrate. Leaves oblong-obovate, more or less cordate and usually not strongly inequilateral at the base, subcuspidate-acuminate at the tip, 20–30 cm. long, 10–14 cm. broad, membranaceous, minutely and closely ciliate-denticulate, both surfaces golden spreading-hirsute but particularly beneath, the petioles about 1 cm. long; stipules 3–6 cm. long. Inflorescences in clusters of 2–4 in catenate series of the upper leaf-axils, occasionally solitary. Staminate heads conduplicate-reniform, about 1.5 cm. long and 2 cm. broad, the peduncle about 1 cm. long. Fruiting heads thickly discoid, 4–5 cm. in diameter, about 1.5 cm. thick, sessile or subsessile, the component flowers half or more coherent, developing an orange or reddish pulp at maturity.

Southern Mexico to Colombia and perhaps southward; in moist forests at low elevations. *Ule-ule, hule, caucho, mastate blanco.*

bocas del toro: Laguna de Chiriquí, *Hart 140*; Chiriquicito, *Seibert 1551*; Punta Rovalo, *Seibert 1566*; Almirante, *Seibert 1574*; Fruit Dale Farm, *Seibert 1586, 1587, 1588.* canal zone: old site of Gorgona, *Maxon 6783*; Las Cascadas Plantation, *Standley 25697, 29497, Cook & Martin 46*; Ancón Hospital grounds, *Maxon 6769, Gaillard s. n.* coclé: El Valle de Antón, *Allen 3625.* darién: along Sambú River, *Pittier 5526*; Boca de Pauarando, *Pittier 5714.* panamá: Río Tapia, *Standley 28048, 26186, 26177*; Juan Días region, *Maxon & Harvey 6748*; Arraiján, *Maxon & Cook 7032, 7033*; Río Tecumen, *Standley 29374*; Tumba Muerto Road, near Panamá, *Standley 29818.*

This species has been of more than passing interest to economic botanists for nearly two centuries, but has never become of commercial value.

2. Castilla tunu Hemsl. in Hook. f. Icon. Pl. ser. 4. 7: *pl. 2651.* 1901.

Castilla fallax Cook, in Science n. ser. 18:438. 1903.

Trees 5–20 m. tall, the young branches densely hirsute with appressed rather dingy-brown hairs, eventually glabrate. Leaves broadly elliptic to oblong-obovate, subcuspidate-acuminate at the tip, obtuse to acuse and very strongly inequilateral at the base, 15–40 cm. long, 7–15 cm. broad, minutely and closely ciliate-denticulate to subentire, membranaceous, appressed-hirsute above and below to glabrate, the petiole about 1 cm. long; stipules 4–5 cm. long. Inflorescences paired or solitary in the upper leaf-axils. Staminate heads conduplicate-reniform, about 2 cm. long and 2.5 cm. broad, sessile or subsessile. Fruiting heads oblate-globose, 2–3 cm. in diameter, quite sessile, the component flowers coherent only toward the base, greenish and nearly dry at maturity.

British Honduras to Panama, in moist forests at low elevations.

darién: Río Chico, near Yaviza, *Allen 4586*; trail between Pinogana and Yaviza, *Allen 276*; Garachiné, *Pittier 5696.* san blas: Puerto Obaldía, *Pittier 4341*; locality indefinite, *Cooper 284.*

This species, according to Allen, "is reported as NOT being used for rubber" in Darien, which Pittier confirms from his experience in Costa Rica. According

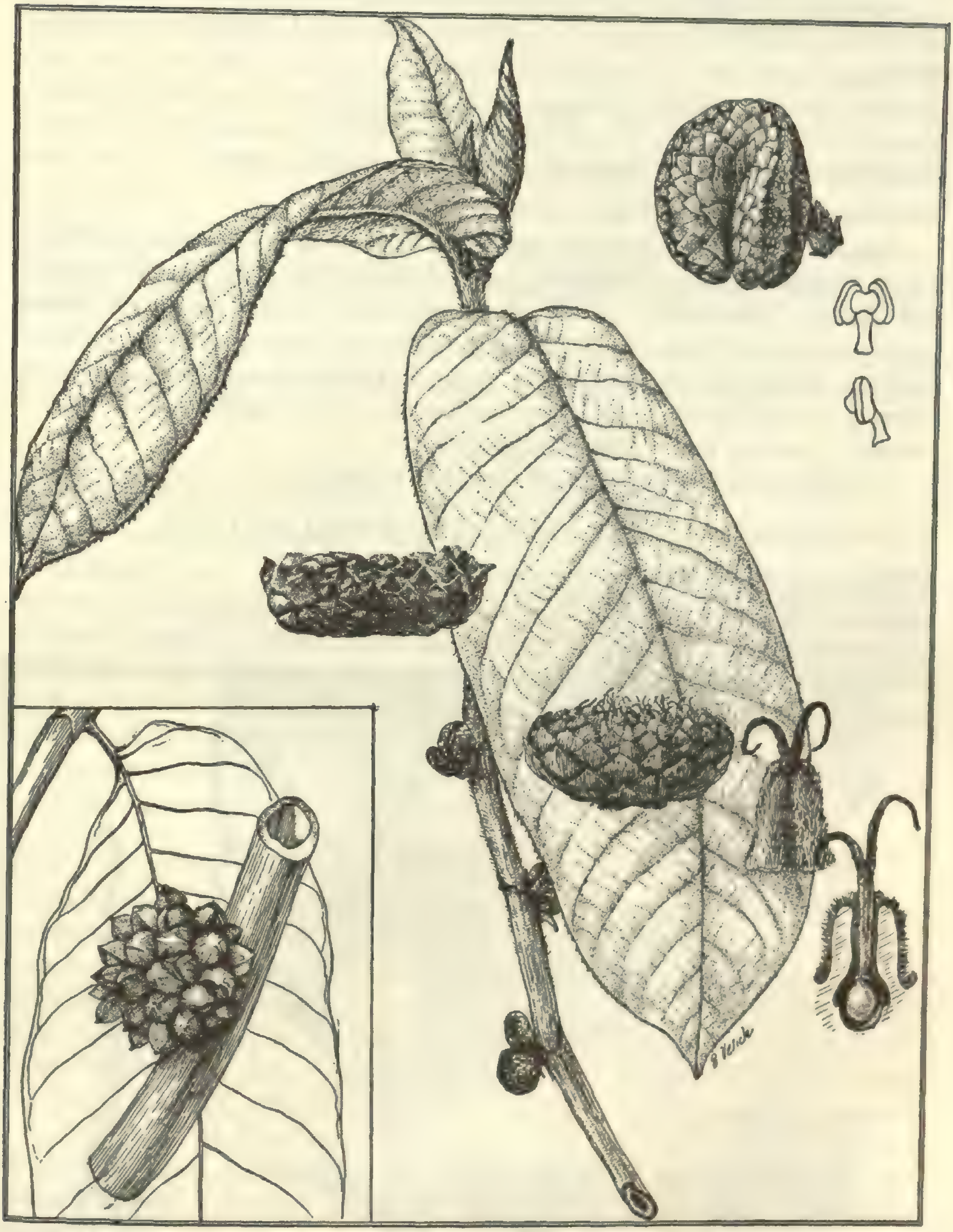

Fig. 50. *Castilla elastica* and *C. tunu* (lower left)

to Pittier, the species also is known to occur in Chiriquí, in the vicinity of David.

In spite of the faults which both Pittier and Cook have found with Hemsley's description and plate, there appears to me little doubt that *C. fallax* is a superfluous name.

9. POULSENIA Eggers

Poulsenia Eggers, in Bot. Centralbl. 73:65 [err. 49]. *pl 3.* 1898.

Inophloem Pittier, in Journ. Wash. Acad Sci. 6:113. 1916.

Monoecious trees, the young branches usually more or less aculeate, rarely unarmed. Leaves alternate, distichous; stipules fully amplexicaul. Both staminate and pistillate inflorescences of globose or subglobose heads. Staminate flowers many: perianth of 4 scarcely united tepals; stamens 4, with broadly oval, basifixed anthers. Pistillate flowers few (3–9): perianths tubular-conic, shortly 4-dentate, strongly coherent in the head; ovary superior, the stigma deeply 2-lobed, widely exserted. Fruiting head a fleshy syncarp.

One species ranging from British Honduras to Bolivia.

1. Poulsenia armata (Miq.) Standl. in Trop. Woods 33:4. 1933.

Olmedia (?) armata Miq. in Seem. Bot. Voy. Herald 196. 1854.
Poulsenia aculeata Eggers, in Bot. Centralbl. 73:66 [err. 50]. 1898.
Inophloem armata (Miq.) Pittier, in Journ. Wash. Acad. Sci. 6:113. 1916.
Coussapoa rekoi Standl. in Contrib. U. S. Nat. Herb. 20:211. 1919.

Fig. 51. *Poulsenia armata*

Trees to 25 m. tall, all young parts scatteringly hispid and aculeate to glabrous and smooth. Leaves broadly and rather obliquely oval or elliptic, the tip obtuse or rounded to shortly subcuspidate-acuminate, the base broadly obtuse, 8–40 cm. long, 4–20 cm. broad, entire, subcoriaceous, the petiole 1–3 cm. long; stipules 2–3 cm. long. Staminate heads globose, without an obvious involucre, many-flowered, about 1 cm. in diameter. Pistillate heads subglobose or ovoid, without an obvious involucre, 3–9-flowered, about 1.5 cm. in diameter. Mature fruiting heads unknown to us.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 88*; Almirante, *Cooper 455*. CANAL ZONE: Alhajuela, *Pittier 3731*; Gatún Valley, *Pittier s. n.*; Barro Colorado Island, *Shattuck 1104, Carpenter 75*. COLÓN: Dos Bocas, Fató Valley, *Pittier 4202*. DARIÉN: Pinogana, *Pittier s. n.*

Pittier reports that the bark is very thick and fibrous and is soaked and pounded into cloth (*mastate*) by the Darién Indians, a use previously reported by Seemann.

10. OLMEDIA R. & P.

OLMEDIA R. & P. Fl. Peruv. & Chil. Prodr. 129. *t. 28.* 1794.

? Maquira Aubl. Hist. Pl. Guian. Fr. Suppl. 2:36; 4: *t. 389.* 1775.

Dioecious trees. Leaves alternate, distichous; stipules wholly amplexicaul. Staminate inflorescences involucrate discoid heads. Staminate flowers definitely organized; perianth campanulate, broadly 4-dentate; stamens 4, the anthers basifixed, oblongoid. Pistillate inflorescences with a solitary prominently bracteate-involucrate flower, the ovary superior, the stigma with 2 widely exserted filiform lobes. Fruit a small slightly fleshy false drupe.

One species in Central America; the South American species are impossible to ascertain at present because of our faulty knowledge.

1. OLMEDIA ASPERA R. & P. Fl. Peruv. & Chil. Prodr. 129. *t. 28.* 1794.

Rather small trees or shrubs to about 6 m. tall, the young twigs rather slender, not conspicuously flexuose, densely to sparsely hispidulous, eventually glabrate. Leaves obovate- or oblanceolate-elliptic, rarely irregularly lyrate, narrowly subcaudate-acuminate at the tip, acutely or obtusely cuneate at the base, frequently more or less falcate, 7–20 cm. long, 2–9 cm. broad, usually more or less conspicuously and irregularly serrate-undulate toward the tip, firmly membranaceous, scabrous or hispidulous to glabrous, the petioles about 5–7 mm. long. Staminate inflorescences solitary or in clusters of 2–4, about 1 cm. in diameter, the peduncles about 5 mm. long. Pistillate inflorescences solitary or in small axillary clusters, the peduncles about 5–7 mm. long, the involucral bracts ovate, 2–4 mm. long, persistent.

BOCAS DEL TORO: Chiriquí Lagoon, *Von Wedel 1043, 1094*; Water Valley, *Von Wedel 896, 941, 1582, 1719*. CANAL ZONE: Gatún, *Pittier 6747, Johnston 1584, Standley 27209*; Quebrada Salamanca, *Steyermark & Allen 17142*; Río Pina–Rio Media divide, *Johnston 1703;* Quebrada La Palma, *Dodge & Allen 17365*; Mindi Hills, *Johnston 1733*; Darién Station, *Standley 31597*; Cerro Gordo, near Culebra, *Standley 26015*; Gorgona, *Maxon*

Fig. 52. *Olmedia aspera*

4744; Barro Colorado Island, *Standley 31450*, *Woodworth & Vestal 372*, *666*, *Wetmore & Abbe 46*, *666*, *Salvoza 930*, *939*, *Bangham 521*, *530*. CHIRIQUÍ: San Félix, *Pittier 5291*; Paso Quebrada Gato, *Pittier 5425*; Hato del Jobo, *Pittier 5425*. COCLÉ: El Valle de Antón, *Allen 1736*. DARIÉN: Pinogana, *Pittier 6578*. PANAMÁ: Río Tecumen, *Standley 29454*; Chepo, *Pittier 4707*.

This is the only Panamanian species of Moraceae where I have been able to find anything comparable to the familiar leaf polymophism of the northern mulberries.

11. PSEUDOLMEDIA Tréc.

PSEUDOLMEDIA Tréc. in Ann. Sci. Nat. 3 ser. 8:129. *t. 5.* 1847.

Olmediopsis Karst. Fl. Colomb. 2:17. *t. 109.* 1862.

Dioecious trees. Leaves alternate, distichous; stipules fully amplexicaul. Staminate inflorescences in discoid involucrate heads of numerous extremely reduced flowers represented by a solitary stamen with an oblongoid basifixed anther

and an extremely vestigial perianth, intermingled with more prominent spatulate bracteoles. Pistillate flowers solitary with an involucre of several closely imbricated bracts, perigynous or epigynous; perianth tubular with 4 minute dentate lobes; stigma narrowly 2-lobed, widely exserted. Fruit a false drupe subtended by the persistent involucre.

4–5 species of the Antilles, Central America and northern and western South America.

1. PSEUDOLMEDIA SPURIA (Sw.) Griseb. Fl. Brit. W. Ind. 152. 1859.

Brosimum spurium Sw. Prodr. 12. 1788.
Pseudolmedia havanensis Tréc. in Ann. Sci. Nat. 3 ser. 8:130. 1847.
Brosimum caloxylon Standl. in Trop. Woods 17:11. 1929.

Trees 8–20 m. tall, the young branches relatively slender, glabrous. Leaves ovate- to oblong-elliptic, rather abruptly and bluntly subcaudate-acuminate to subcuspidate, the base obtuse to rounded, firmly membranaceous to subcoriaceous, entire, 9–15 cm. long, 3–5 cm. broad, glabrous or essentially so, the petiole 3–5 mm. long; stipules vary narrowly lanceolate, long-acuminate, 1–2 cm. long. Staminate heads usually paired, sessile or subsessile, about 8–10 mm. in diameter, the bracts broadly obtuse, minutely puberulent. Pistillate heads sessile, the flowers ovoid, about 2 mm. long, softly puberulent, the stigma lobes about equally long. Drupes broadly ovoid, fleshy, about 1 cm. long and broad.

British Honduras to northern South America; Antilles. Reported as *cuqua* by Cox, bloodwood and *cacique* by Proctor Cooper.

BOCAS DEL TORO: Buena Vista Camp on Chiriquí Trail, *Cooper 607*; "Bocas del Toro Region", *Cox s. n.*; Cricamola Valley, *Cooper 535*.

All three collections are quite sterile, hence their assignment to this species is not infallible. It is true that these leafy sheets could be matched fairly well by some South American species of *Brosimum* or even *Ficus*. But this guess appears to be quite the most likely.

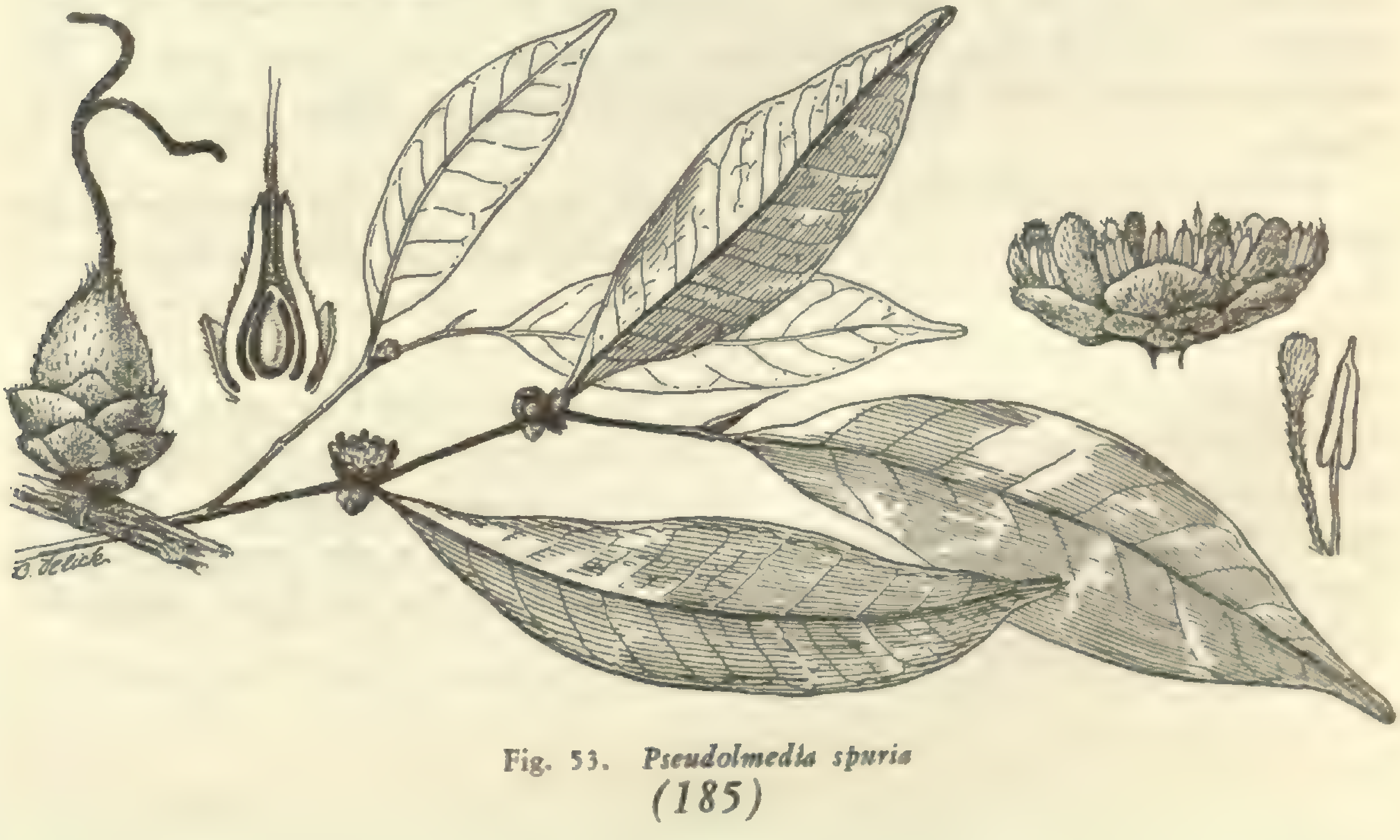

Fig. 53. *Pseudolmedia spuria*

12. FICUS [Tourn.] L.

By GORDON P. DEWOLF, Jr.

Ficus [Tourn.] L. Gen. Plant. ed. 5. 482. 1754.

Oluntos Raf. Sylva Tell. 58. 1838.
Urostigma Gasp. Nov. Gen. Fic. 7. 1844.
Pharmocosycea Miq. in Hook. Lond. Journ. Bot. 7:64. 1848.
(Synonyms not referring to American species not cited.)

A genus (at least so far as the American species are concerned) of soft-wooded, generally smooth-barked trees and shrubs with milky or opalescent latex. Many species begin life as epiphytes, or epiliths, which may eventually, through the coalescence of their roots, completely encircle the trunk of, and strangle, their host. Leaves entire and spiral in native species—rarely opposite and sometimes toothed or lobed in the Old World. Stipules long or short, enfolding the buds, generally quickly deciduous but rarely persistent, leaving a scar surrounding the stem. Flowers unisexual, borne over the inner surface of a hollow, globose, more or less fleshy structure (the receptacle or "fig") the apical pore (ostiole or orifice) of which is closed by a series of interlocking bracts. The female flowers are of two kinds: functional females, generally sessile and maturing into viable achenes, and sterile females (gall flowers), generally stalked and functioning as incubators for the larvae of a wasp which pollinates the fertile flowers. Male, female and gall flowers are completely intermixed in American species. The figs are generally solitary or paired, borne among the leaves but sometimes on specialized short shoots behind the leaves in American species. In Old World species they may be borne similarly or in leafless racemes or panicles on the trunk and larger branches.

There are about 750 species in the tropics of both hemispheres. In the American tropics the genus is represented by two subgenera (of three) and about 70 species. In addition to the native species of Panama, numerous exotics are cultivated, particularly *F. elastica*, *F. nitida* and the banyan, *F. religiosa*, and the root-climbing ivy-like *F. pumila*. These usually can be distinguished by their persistent aerial and prop roots which are infrequent in the native species. The common edible fig with deeply lobed leaves, *F. carica*, is seldom encountered in Panama.

Subgenus urostigma (Gasp.) Miq. Most species of fig are disseminated by birds which eat the more or less fleshy receptacles and wipe their beaks clean of the sticky pulp upon the branch of a convenient tree. The small seeds embedded in the pulp deposited in this way germinate epiphytically, the seedlings grasping the supporting tree with their tentacles of aerial roots which in time reach the soil. Meanwhile the woody body of the fig develops rapidly and the supporting tree eventually is destroyed by the weight of its triumphant epiphyte. For this reason the name *matapalo* (tree-killer) often is applied to the strangler-figs of Central America. The appropriate Spanish words *higo* for the fleshy receptacles and *higuero* for the tree are current in Panama.

Subgenus PHARMACOSYCEA Miq. The Pharmacosyceas seldom, if ever, begin life as epiphytes. They are large, free-growing trees of the forest and of second growth. The subgenus was originally erected for a few American species but it is now known that about 46 Australasian species belong here as well.

In any consideration of a taxonomic treatment of tropical American plants it is important to realize that botanically scarcely one quarter of tropical America has been adequately explored. Literally thousands of square miles of rainforest and *campo* have either never been investigated by botanists or have not been so for fifty to one hundred years. Even so, our herbaria are full of alleged species whose only claims to distinction, when they are examined critically, are the political boundaries separating them.

With the exception of the West Indies, Mexico, parts of Central America and some areas in northern South America, what knowledge we have of the lowland evergreen forests seems to be restricted to the vegetation of the riverbanks. In addition, few, even of modern collectors, have bothered to make field notes—or, if they have made them, have not bothered to transcribe them onto labels to accompany their specimens. The net result is that, although there is a good deal of (literally scrappy) material in our herbaria, we can get only the most vague idea either of distribution or of variation of the species involved, and we know practically nothing of the ecology of the plants. As a final example and indictment, *Ficus nymphaeaefolia* is apparently a fairly common species from Panama to the State of Amapa in Brazil at the mouth of the Amazon. Even as tropical trees go, it must be striking in appearance. Yet the only description of this species as a living plant that I have been able to find is in Humboldt's "Personal Narrative . . ." of his travels in the American tropics in 1799–1804.

The floral characters of American figs, unlike those of many Asian and African species are disconcertingly uniform. The precise form and structure of the fig itself is, however, particularly significant. In addition, microscopic vegetative characters have considerable taxonomic significance. These characters were first investigated by Otto Renner in 1907. More recently they have been exploited and practical techniques for their elucidation devised by Professor E. J. H. Corner, to whom I am greatly indebted for knowledge of them.

Over the past three years I have been able to see nearly all of the types of American species of *Ficus* preserved in European herbaria. More than a year ago, I was able to present to the Board of Research Studies of the University of Cambridge a taxonomic and nomenclatural revision of the species of *Ficus*, proposed on the basis of allegedly American material from the time of the publication of the Species Plantarum in 1753 to the first proper taxonomic revision of the genus by Miquel in 1847-48. This involved a taxonomic study of all the species known from Brazil, northeastern South America and the West Indies, as well as a cursory survey of the species of the Andes and of Central America and Mexico.

Over and above the courtesies extended to me by the directors and staffs of all institutions that I have visited or corresponded with (which will be acknowledged

explicitly in a forthcoming paper), I am particularly indebted to the directors of the New York Botanical Garden and the United States National Museum, who allowed me to borrow certain specimens in their care to use as a basis for study of the taxonomy of the species. I am also in particular debt of gratitude to the American Academy of Arts and Sciences who generously made a grant to allow me to visit certain continental herbaria, to consult the types in their care.

Some months ago, Dr. R. E. Woodson, Jr., hearing of my interest in the genus, sent me for comment a manuscript treatment which he had prepared for the FLORA OF PANAMA. It is a pleasure to record that, with one or two minor exceptions, our taxonomic conclusions were identical. After some subsequent correspondence, Dr. Woodson asked me to prepare a fresh treatment of *Ficus* for the Flora. The following descriptions and synonomy are the result. I have seen little Panamanian material for any species. The descriptions are drawn from the material which I have seen, modified freely from Dr. Woodson's manuscript. The specimens cited are quoted directly from that manuscript. The nomenclature and synonymy are based (with one or two exceptions) on my own studies.

a. Figs borne singly in the leaf axils, the bracts at the base of fig 3 or 3-lobed; stamens 2; ovary pale, unspotted; tepals of female flowers narrowly deltoid or lanceolate; massive multicellular hairs present (× 150) on the lower surface of the leaf. (Subgenus PHARMACOSYCEA)
  b. Stipules 1–2 cm. long; lateral veins of the leaves 5–16; lower surface of the leaves minutely pubescent to glabrous, almost always scabrid. 1. F. MAXIMA
  bb. Stipules 2.5 cm. or more long.
    c. Leaves very broadly oval or ovate, the lateral veins 10–16, rather distant; receptacles not beaked.
      d. Lateral veins 9–15, departing from the midrib at an angle of 10° or less, connected by a very prominent submarginal vein..... 2. F. TONDUZII
      dd. Lateral veins 12–16, departing from the midrib at an angle from 10°–30°, the marginal vein not prominent.......... 3. F. MACBRIDEI
    cc. Leaves oblong-elliptic, the lateral veins 10–30, rather close; receptacles generally somewhat beaked below the ostiole.......... 4. F. INSIPIDA
aa. Figs borne in pairs in the leaf axils, the basal bracts 2 or 2-lobed; stamen 1; ovary with a red spot at the base of the style; tepals of all flowers hooded; massive, multicellular hairs absent, 2-cellular glandular hairs (×150) frequently present on the lower surface of the leaf. (Subgenus UROSTIGMA)
  b. Figs cylindrical, to 20 mm. long, with densely spreading yellow-brown pubescence. .... 5. F. POPENOEI
  bb. Figs more or less globose, glabrous or pubescent.
    c. Mature figs 3–7 mm. in diameter.
      d. Stipules glabrous; figs distinctly pedunculate.......... 6. F. PERFORATA
      dd. Stipules appressed-pubescent; figs sessile or nearly so.
        e. Leaves smooth above, appressed-pubescent on the veins beneath. 7. F. HARTWEGII
        ee. Leaves scabrid above, shortly spreading-pubescent beneath....... 8. F. DENDROCIDA
    cc. Mature figs 8–30 mm. in diameter.
      d. Figs with a distinct peduncle.
        e. Ostiole sunken into the body of the fig or surrounded by a more or less raised collar of receptacular tissue or both.
          f. Figs and leaves glabrous.
            g. Ostiole depressed within a relatively undifferentiated cavity.......... 9. F. PERTUSA
            gg. Ostiole depressed within a conspicuously elevated cylindrical collar. ....10. F. TRACHELOSYCE
          ff. Figs and leaves spreading-pubescent..........11. F. BULLENEI
        ee. Ostiole level with the surface of the fig, or the bracts slightly umbonate.

f. Figs 8–15 mm. in diameter, with thin wall, yellowish when ripe.......12. F. CITRIFOLIA
ff. Figs 15–30 mm. in diameter, with a relatively thick wall, reddish when ripe.......13. F. TRIGONATA
dd. Figs sessile or nearly so.
e. Figs 15–30 mm. in diameter.
f. Bracts at mouth of fig distinctly mammillate, to 3 mm. high, leaves oblong-oblanceolate, distinctly acuminate, base rounded, lateral veins 9–18.......14. F. PARAENSIS
ff. Bracts at mouth of fig level with the surface or only a little umbonate, leaves rotund to broadly oval or elliptic-oblong or oblanceolate, apex rounded to acuminate, base narrowly cuneate to cordate, lateral veins 4–12.
g. Leaves rotund, very broadly oval or ovate, apex rounded to acuminate, the base distinctly and deeply cordate.......15. F. NYMPHAEAEFOLIA
gg. Leaves ovate to oblanceolate, apex rounded to obscurely acuminate, base cuneate or rounded, sometimes emarginate.
h. Leaves ovate to oblong-elliptic, apex rounded to obscurely acuminate, base rounded to emarginate.......13. F. TRIGONATA
hh. Leaves oblanceolate to obovate, apex rounded to acute, base narrowly cuneate.......16. F. OBTUSIFOLIA
ee. Figs 8–14 mm. in diameter.
f. Bracts at mouth of fig distinctly mammillate, to 3 mm. high, leaves oblong-oblanceolate, distinctly acuminate, base rounded, lateral veins 9–18.......14. F. PARAENSIS
ff. Bracts at mouth of fig level with the surface or only a little umbonate, leaves not as above, apex rounded to obscurely acuminate, base cuneate to rounded, lateral veins 5–12.
g. Stipules persistent.......17. F. COSTARICANA
gg. Stipules deciduous.
h. Stem at each receptacle-bearing node enlarged to form a shelf or socket on which figs are borne, basal bracts fused to the base of fig for about 5 mm.......18. F. TUERCKHEIMII
hh. Stem not enlarged at the nodes, basal bracts not fused to the base of the fig.
i. Leaves oblong-obovate or oblanceolate.
j. Stipules about 10 mm. long, figs 8–10 mm. in diameter.......19. F. DAVIDSONAE
jj. Stipules 10–30 mm. long, figs more than 10 mm. in diameter.......16. F. OBTUSIFOLIA
ii. Leaves elliptic or obovate, stipules 15–30 mm. long, figs 10–14 mm. in diameter.......13. F. TRIGONATA

1. FICUS MAXIMA P. Mill. Gard. Dict. ed. 8 (*Ficus* no. 6). 1768.

Ficus citrifolia hort. ex Lamck. Encycl. Meth. (Bot.) 2:494. 1786, quoad syn. excl. typus (in herb. Lamarck).
Ficus laurifolia hort. ex Lamck. loc. cit. 2:495. 1786, quoad syn. excl. typus (spec. in herb. Desfontaines).
Ficus virens Dryand. in Ait. Hort. Kew. ed. 1. 3:451. 1789, quoad syn. excl. typus.
Ficus anthelminthica Rich. ex DC. Ess. Pl. Med. 267. 1804 (fide herb. Richard), nom. nud.
Ficus martinicensis Willd. Sp. Pl. ed. 4. 4^2:1137. 1806, quoad syn. excl. typus.
Ficus radula H. & B. ex Willd. loc. cit. 1144. 1806.
Pharmacosycea grandaeva Mart. ex Miq. in Hook. Lond. Journ. Bot. 7:70. 1848.
Pharmacosycea guyanensis Miq. loc. cit. 67. 1848.
Pharmacosycea glaucescens Liebm. in Kong. Danske Vidensk. Selsk. Skr. ser. 5. 2:332. 1851.
Pharmacosycea hernandezii Liebm. loc. cit. 1851.
Pharmacosycea rigida Miq. in Seem. Vot. Voy. Herald. 195. 1854, nec Desf. nec Jack.
Pharmacosycea mexicana Miq. in Versl. en Med. Kon. Akad. Wetensch. 13:415. 1862.
Pharmacosycea pseudoradula Miq. loc. cit. 414. 1862.
Ficus suffocans Griseb. Fl. Brit. W. Ind. 150. 1864.
Ficus glaucescens (Liebm.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3:300. 1867.

Ficus hernandezii (Liebm.) Miq. loc. cit. 1867.
Ficus parkeri Miq. loc. cit. 1867.
Ficus mexicana (Miq.) Miq. loc. cit. 299. 1867.
Ficus pseudoradula (Miq.) Miq. loc. cit. 1867.
Ficus coybana Miq. loc. cit. 300. 1867.
Ficus guadalajarana S. Wats. in Proc. Amer. Acad. 26:151. 1891.
Ficus finlayana Warb. in Urb. Symbol. Antill. 3:487. 1903 (pro parte).
Ficus picardae Warb. loc. cit. 484. 1903.
Ficus rubricosta Warb. loc. cit. 486. 1903.
Ficus subscabrida Warb. loc. cit. 485. 1903.
Ficus ulei Warb. ex Ule, in Engl. Bot. Jahrb. 40:141. 1907, nom. nud.
Ficus plumieri Urb. in Fedde, Repert. 15:158. 1918.
Ficus hopiana Rusby, in Mem. N. Y. Bot. Gard. 7:230. 1927.
Ficus ulei Rossb. in Fedde, Repert. 42:60. 1937.
Ficus vicencionis Dugand, in Caldasia 2:385–386. 1944.

Small to large trees 5–30 m. tall. Twigs 3–5 mm. in diameter, glabrous or pubescent, with a thin, scurfy, yellowish brown periderm. Stipules to 25 mm. long, narrowly deltoid, glabrous, puberulent, or pubescent at the base. Lamina 2.5–12 cm. wide × 6–24 cm. long, elliptic, broadly elliptic, lanceolate, oblanceolate, or obovate, glabrous above, glabrous or puberulent beneath; apex blunt, acute, acuminate or long acuminate; base cuneate or obtuse; lateral veins 5–16 pairs, departing from the midrib at an angle from 0°–30°; basal veins departing from the midrib at an angle of 40°–60°; intercostals slightly raised. Petiole 5–40 mm. long, ⅕–⅑ the length of the lamina, the epidermis generally scurfy. Figs 10–25 mm. in diameter, globose, or sub-globose, glabrous or puberulent, sometimes with a stalk above the basal bracts 2–7 mm. long, borne among the leaves; color green or yellow, sometimes mottled darker; peduncle 2–25 mm. long, glabrous or pubescent; basal bracts 1–2 mm. long, deltoid, glabrous or pubescent; orifice 1–2 mm. in diameter, flat, or the bracts slightly outflexed.

Southern Mexico to and through the Amazon basin, lowlands to about 1000 ft.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 92, Dunlap 498*. CANAL ZONE: south of Ft. Sherman, *Johnston 1656*; Balboa, *Standley 25611, 27006*; Corozal, *Standley 26829*; Ancón, *Pittier 2728*; Culebra, *Pittier 2211*. COCLÉ: Penonomé, *Williams 251*. PANAMÁ: San José Island, *Johnston 449, 533, 1338, 1383*; Taboga Island, *Standley 27976*; Chepo, *Pittier 4757*; Juan Días, *Standley 30481*.

This seems to be a relatively common species in lowland forest and in lowland hill forest from Cuba and southern Mexico to, and through, the Amazon basin. In the low mountain rain forest in Jamaica this species occasionally overtops the forest canopy (Apsey, 1953), and it forms an element of the flora which springs up on waste land left after removal of bauxite in western Jamaica (Howard and Proctor, 1957).

Despite the multitude of names which have been proposed for various examples of this species, it does not seem to be particularly variable. There is, of course, considerable variation in leaf size (which is reflected, at least to some extent, in lateral vein number) between young and old plants and shoots, and, of course, leaves from vigorous shoots seem to be generally more strongly acuminate than leaves from mature twigs.

The oldest legitimate name for this species as here defined is *Ficus maxima* Mill.

There is no specimen from Miller's herbarium in the British Museum (NH), so the name must be typified on *Ficus indica maxima, folio oblongo*... of Sloane's "Catalogus..." 189 (1696) and "Voyage..." 2:140, *t. 223* (1725). There is no specimen in the Sloane collection at the B.M. (NH) and the illustration is certainly not diagnostic, but the description is good and sufficiently specific, so that I have no hesitation in designating it the nomenclatural type of Miller's name and following Fawcett and Rendle (Fl. Jam. 3^1:48–49. 1914) in referring it to the plant which for a century has been known as *Ficus suffocans* Griseb.

Ficus protensa (Griseb.) Hemsl. was included in the synonymy of *Ficus glaucescens* by Standley, but I do not know on what grounds. No type was cited in the original description and I have no record of having seen a specimen so labeled. The description is certainly not diagnostic of this taxon. I think that it is unwise to doubt Grisebach's assignment of his plant to the subgenus UROSTIGMA without being able to demonstrate his error from the original material.

I have not seen authentic material of *Ficus guadalajarana*, S. Wats. It is included here on the authority of Dr. Woodson. I have seen the types of all the other names.

2. FICUS TONDUZII Standl. in Contrib. U. S. Nat. Herb. 20:8. 1917.

Ficus macrocyce Pittier, sensu Dugand.

Large buttressed trees to about 15 m. tall. Twigs 4–7 mm. in diameter, glabrous, the epidermis frequently exfoliating, with a thick greyish brown periderm. Stipules 25–60 mm. long, narrowly deltoid, glabrous. Lamina 6–15 cm. wide × 12–30 cm. long, broadly ovate, elliptic or obovate; apex rounded acute, acute or very shortly and bluntly acuminate; base rounded or rounded cuneate; lateral veins sometimes very broad and conspicuous, 9–15 pairs, departing from the midrib at an angle of 10° or less; intercostals conspicuous, but not much raised; basal veins departing from the midrib at an angle of 15°–30°, continuous with the very conspicuous submarginal vein. Petiole 20–80 mm. long, 4–5 mm. thick, ½–⅙ the length of the lamina. Figs 20–35 mm. in diameter, globose, glabrous or minutely scabrid, borne among the leaves; color not noted; peduncle obsolete to 10 mm. long, sometimes with a stalk above the bracts to 5 mm. long; basal bracts 2–3 mm. long, very broadly deltoid; ostiole about 2 mm. in diameter, plane with the surface of the receptacle, or produced in a beak 5–10 mm. high.

Costa Rica to northern Colombia, near sea level to about 640 m.

CANAL ZONE: Barro Colorado Island, *Wetmore & Abbe 303*, *Carpenter 5*, *Shattuck 199*; Obispo, *Standley 31706*. CHIRIQUÍ: Hiquerón, *Cooper & Slater 249*.

3. FICUS MACBRIDEI Standl. in Publ. Field Mus. Nat. Hist. (Bot.) 13:305. 1937.

Ficus torresiana Standl. loc. cit. 18:307. 1937.

Trees to 15 m. tall. Twigs 7–9 mm. in diameter, glabrous or very shortly brown-pubescent, the epidermis sometimes exfoliating. Stipules 50–75 mm. long, narrowly deltoid, glabrous or minutely pubescent. Lamina 12–28 cm. broad × 26–42 cm. long, broadly ovate; apex acute or slightly acuminate; base rounded or

emarginate; lateral veins 12–16 pairs departing from the midrib at an angle of 10°–30°; basal veins 1–3 pairs, departing from the midrib at a similar angle or at an angle from 30°–50°; intercostals slightly prominent. Petiole 20–85 mm. long, glabrous or pubescent, ½–⅙ the length of the lamina. Figs 15–25 mm. in diameter, obovoid, glabrous or pubescent, borne among leaves(?); color not noted, but in dried material with yellowish maculations; peduncle obsolete; basal bracts 2–3 lobed, about 2 mm. long; orifice about 2 mm. in diameter, slightly crateriform.

This species, so far as I know, has not yet been found in Panama. It is found in Costa Rica and Peru, however, and should be looked for in areas between.

4. Ficus insipida Willd. Sp. Pl. ed. 4. 4:1143. 1806.

Ficus glabrata HBK. Nov. Gen. & Spec. 2:47. 1818.
Ficus adhatodaefolia Schott, ex Spreng. Syst. Veg. ed. 16. 4 (App.):409. 1827.
Ficus anthelminthica Mart. in Spix et Mart. Reise in Brasilien 3:1158. 1831.
Pharmacosycea vermifuga Miq. in Hook. Lond. Journ. Bot. 7:70. 1848.
Pharmacosycea angustifolia Liebm. in Kong. Danske Vidensk. Selsk. Skr. ser. 5. 2:333. 1851.
Ficus vermifuga (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3:300. 1867.
Ficus segoviae Miq. loc. cit. 1867.
Ficus radulina S. Wat. in Proc. Am. Acad. 26:151. 1891.
Ficus krugiana Warb. in Urb. Symbol. Antill. 3:487. 1903.
Ficus crassiuscula Warb. ex Standl. in Contrib. U. S. Nat. Herb. 20:12. 1917.
Ficus werckleana Rossb. in Fedde, Repert. 42:60. 1937.
Ficus boyacensis Dugand, in Caldasia 1^4:31. 1942.
Ficus crassa Kl. & Karst. ex Dugand, in Caldasia, 1^4:35–36. 1942.
Ficus mexicana auct. non Miq.

Large or small buttressed trees, 8–40 m. tall. Twigs 2–6 mm. in diameter, generally glabrous, with a thin reddish or greyish brown periderm. Stipules 30–125 mm. long, narrowly deltoid, generally glabrous. Lamina 2–11 cm. wide × 5–25 cm. long, lanceolate to broadly elliptic, essentially glabrous, generally glossy above, sometimes slightly inequilateral; apex blunt or acute, to acuminate; base cuneate, round cuneate, rounded or emarginate; lateral veins 10–25 [–30] pairs, departing from the midrib at an angle of 40° or less; basal veins departing from the midrib at an angle from 30°–60°; intercostals slightly prominent. Petiole 10–65 mm. long, ⅓–⅛ the length of the lamina, the epidermis not exfoliating, though frequently wrinkled. Figs 15–30 mm. in diameter, globose with or without a stalk above the basal bracts, 1–6 mm. long, glabrous or pubescent, borne among the leaves; color green or yellowish-green; peduncle 3–22 mm. long, thin or stout; basal bracts three, 1–3 (–5) mm. long, deltoid or semicircular; orifice flat, or somewhat crateriform or mammillate, 2–4 mm. in diameter, 1–2 mm. high.

Southern Mexico to Southern Brazil, in lowland forests.

BOCAS DEL TORO: Almirante, *Cooper 444*. CANAL ZONE: upper Chilibre River, *Seibert 1512*; Ancón, *Piper 6006*; Chagres River, *Muenscher 12284, 12291*; Ft. Sherman, *Johnston 1510*; Barro Colorado Island, *Bailey & Bailey 479, Carpenter 3, Standley 40931, Wetmore & Abbe 126*. CHIRIQUÍ: Río Dupí, *Pittier 2539*. COLÓN: Río Fató, *Pittier 3880*. DARIÉN: Boca de Cupe, *Williams 679*; Yaviza, *Allen 4589*.

This is, undoubtedly, the most widely distributed of the Pharmacosyceas, though with the exception of one doubtful record it does not occur in the West Indies. It ranges, on the continent, from northwestern Mexico to Paraguay. In Mexico

and Central America it seems to be a component of the arid or sub-arid forests—but, since Standley notes that figs are usually left standing when forests are cleared and since much of the accessible forest of Central America and Mexico is not virgin, it seems unwise to try to guess as to the natural habitat. Standley records, of the populations which he called "*mexicana*," that they were stranglers. This is, presumably, a very unusual state of affairs for any plant of this subgenus.

Both Dugand (Caldasia 3^{12}:133–148. 1944) and Little (in sched.) report the use of the latex of this species as a vermifuge in Colombia. The south Brasilian vernacular name *figueira purgante* and Miquel's epithet *vermifuga* for material from this same area, suggests that its medicinal usage is widespread. In addition, Archer (in sched.) records that Pará the latex is sometimes used in the coagulation of the latex of *Hevea*.

5. FICUS POPENOEI Standl. in Field Mus. Publ. Bot. 4:301. 1929.
Ficus tolimensis Standl. loc. cit. 17:177. 1937.

Trees to 25 m. tall. Twigs 4–6 mm. in diameter, fulvous spreading pubescent, eventually glabrate and developing a moderately thick greyish brown periderm. Stipules about 10 mm. long, densely spreading fulvous pubescent. Lamina 5–15 cm. long × 4–10 cm. wide, broadly oval to obovate-oblong, pubescent below and scabrid above; lateral veins 5–9 (–10) pairs, departing from the midrib at an angle of 20°–40°; basal veins departing at a similar angle; intercostals somewhat prominent. Petiole 5–15 mm. long, pubescent, $\frac{1}{6}$–$\frac{1}{16}$ the length of the lamina. Figs 14–22 mm. long × 9–16 mm. in diameter, cylindric, pubescent, borne among the leaves; color green, brown tinted (yellow-brown pubescent in dried material); peduncle 3–5 mm. long, pubescent; basal bracts broadly deltoid about 2–5 mm. long, pubescent; orifice about 2 mm. in diameter, flat or very slightly umbonate.

Fig. 54. *Ficus popenoei*

British Honduras to central Colombia, in lowland forests.

COCLÉ: El Valle, *Allen 3789, Harvey 5169*. PANAMÁ: San José Island, *Johnston 483, 640, 660, 804*.

Dr. Johnston reports that the habit of this species is quite variable: some may be stranglers, while others may germinate in the soil; a few develop a banyan-like stilted habit, but this is exceptional.

This seems to be a relatively common plant in Central America which has been identified, in the past, as *Ficus velutina*. There may be some vegetative similarity, but the cylindrical, densely yellow-brown pubescent figs are quite distinctive.

6. Ficus perforata L. Pl. Surin. 17. 1775.

Ficus americana Aubl. Pl. Guian. 2:952. 1775.
Ficus jacquiniaefolia A. Richard. Fl. Cub. Fanerog. 3:221. *t. 72.* 1850.
Urostigma eugeniaefolium Liebm. in K. Danske Vid. Selsk. Skrivt. 5 ser. 2:329. 1851.
Urostigma oerstedianum Miq. in Seem. Bot. Voy. Herald 196. *t. 36.* 1854.
Urostigma liebmannianum Miq. loc. cit. 195. 1854.
Urostigma chiriquianum Miq. in Versl. en Med. Kon. Akad. 13:412. 1862.
Ficus chiriquiana (Miq.) Miq. in Ann. Mus. Bot. Lugd.-Bat. 3:298. 1867.
Ficus liebmanniana (Miq.) Miq. loc. cit. 1867.
Ficus oerstedianum (Miq.) Miq. loc. cit. 299. 1867.
Ficus eugeniaefolia (Liebm.) Hemsl. Biol. Centr.-Amer. Bot. 3:144. 1883.
Ficus sintenisii Warb. in Urb. Symbol. Antill. 3:464. 1903.
Ficus omphalophora Warb. loc. cit. 466. 1903.
Ficus wilsoni Warb. loc. cit. 467. 1903.

Shrubs or small to medium sized trees to 30 m. tall. Twigs 2–3 mm. in diameter, glabrous, with a rather close brownish grey periderm. Stipules 4–15 mm. long, glabrous, ciliolate or glaucous. Lamina 1–5 cm. wide × 1.7–11 cm. long, elliptic or obovate; apex rounded, acute, or short, abruptly acuminate; base cuneate or narrowly rounded, sometimes somewhat emarginate; lateral veins 6–14 pairs, departing from the midrib at an angle from 20°–30°; basal veins departing from the midrib at a similar angle; intercostals not, or only somewhat, prominent. Petiole 4–10 mm. long, ¼–⅑ the length of the lamina. Figs 3–7 mm. in diameter, globose, glabrous, borne among the leaves; color reddish; peduncle 1–5 mm. long, glabrous or minutely puberulent; basal bracts two, 1–2 mm. long, ovate, glabrous or minutely puberulent; orifice 1–2 mm. in diameter, somewhat mammillate.

Guatemala to Colombia, at intermediate or higher elevations; and in the Bahama Islands and the Greater Antilles. *Mata palo.*

CANAL ZONE: Barro Colorado Island, *Wilson 122, Carpenter 64, Woodworth & Vestal 658, Bangham 509.* CHIRIQUÍ: Gualaca, *Allen 5026*; Boquete, *Davidson 612*; Caldera, *Pittier 3346*; David, *Pittier 2822, 2823.* COCLÉ: El Valle, *Allen 2228.* DARIÉN: Cana, *Williams 944.* PANAMÁ: Punta Paitilla, *Standley 26243.* VERAGUAS: Río Cañazas, *Allen 158.*

This is an exceedingly variable taxon, the West Indian plants called *Ficus jacquiniaefolia* and *F. sintenisii* being, superficially, very different in appearance. There is, however, no important character by which they can be circumscribed and it seems wise, therefore, to include them here.

Ficus perforata L. is based on *t. 132, f. 2.* of Burmann's edition of Plumier's plates. Neither Warburg nor Urban were sure of the identity of the plant, but I believe that Warburg was correct in suggesting that it is the plant which he called *F. omphalophora,* the common shrubby fig of the Lesser Antilles. *F. wilsoni* of Jamaica is indistinguishable, save only that the stomates are somewhat larger.

7. Ficus hartwegii (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3:299. 1867.

Urostigma hartwegii Miq. in Hook. Lond. Journ. Bot. 6:545. 1847.
Ficus colubrinae Standl. in Contrib. U. S. Nat. Herb. 20:16. 1917.

Trees, 10–35 m. tall. Twigs 3–4 mm. in diameter, appressed pubescent to

glabrate, soon developing a rather thin yellowish brown periderm. Stipules to 20 mm. long, deltoid, appressed pubescent. Lamina 2.5–8 cm. wide × 3.5–13.5 cm. long, broadly elliptic or obovate, appressed pubescent on the veins; apex short abrupt acuminate; base rounded, emarginate or cuneate; lateral veins 4–6 (–8) pairs, departing from the midrib at an angle from 20°–30° (–40°); basal veins departing from the midrib at an angle from 30°–40° (–60°); intercostals only slightly prominent. Petiole 6–30 mm. long, (¼–) ⅕–⅐ the length of the lamina, appressed pubescent. Figs 6–7 mm. in diameter, globose, glabrous, borne among the leaves; color pale red; peduncle obsolete; basal bracts two, to 2 mm. long, semicircular, pubescent; ostiole to 2 mm. in diameter, plane in a very slight rim of receptacular tissue.

Guatemala and British Honduras to Colombia, in lowland forests and thickets.

BOCAS DEL TORO: Old Bank Island, *Von Wedel 1999*; Cricamola Valley, *Cooper 519*; Almirante, *Cooper 404*. CANAL ZONE: Fort Sherman, *Johnston 1626, 1748, Standley 31122*; Fort Randolph, *Standley 28676*; France Field, *Standley 30339*; Barro Colorado Island, *Shattuck 239, Carpenter 20, Woodworth & Vestal 571, Kenoyer 319*. COCLÉ: El Valle de Antón, *Allen 2000, 2478, 2889*.

The basal veins appear to be three but are accompanied on either side by a pair of very inconspicuous nerves.

According to Dugand (Caldasia 2^9:274–275. 1943) this is an extremely common fig in the central Andes of Colombia between 500 and 1600 m. altitude.

8. FICUS DENDROCIDA HBK. Nov. Gen. & Spec. Pl. 2:46. 1817.

Ficus elliptica HBK. loc. cit. 1817.
Ficus arboricida Schult. Mantissa 1:331. 1822.
Ficus dendroctonia Spreng. Syst. Veg. ed. 16. 3:780. 1826.

Large spreading trees, to 30 m. tall, frequently with many air roots. Twigs 2–3 mm. in diameter, pubescent, developing a rather thick dark brown periderm. Stipules 5–8 mm. long, narrowly deltoid, appressed pubescent. Lamina 2.5–5 cm. wide × 5–8.5 cm. long, elliptic or slightly obovate, scabrid above, pubescent beneath; apex acute; base rounded; lateral veins 5–8 (–12) pairs, departing from the midrib at an angle from 30°–40°; basal veins departing from the midrib at an angle 30°–50°; intercostals somewhat raised. Petiole 6–15 mm. long, ⅕–⅒ the length of the lamina. Figs 5–6 mm. in diameter, globose, pubescent or glabrescent, borne among the leaves; color not noted; peduncle obsolete; basal bracts 1–2 mm. long, connate, semicircular, pubescent; ostiole 1–2 mm. in diameter, flat.

Panama and Colombia, perhaps to northern Brazil.

PANAMÁ: margins of tidal swamp, Pacora, *Allen 3446*.

This is a species which seems to be almost completely confined to the drainage of the Río Magdalena in Colombia, below 700 m. altitude. What little we know of its variation is due to the efforts of Dr. A. Dugand (Caldasia 2^8:169–171. 1947), who notes that it is extremely variable in size, shape, texture and pubescence of the leaves.

9. Ficus pertusa L. f. Suppl. Plant. 442. 1781.

Ficus padifolia HBK. Nov. Gen. & Sp. 2:47. 1817.
Ficus complicata HBK. loc. cit. 48. 1817.
Ficus ciliolosa Link, Enum. Pl. Berol. 2:450. 1822.
Ficus myrtifolia Link, loc. cit. 1822.
Ficus arbutifolia Link, loc. cit. 1822.
Ficus cestrifolia Schott, ex Spreng. Syst. Veg. ed. 16. 4 (App.):409. 1827.
Ficus lancifolia Hook. et Arn. Bot. Beech. Voy. 310. 1841.
Ficus subtriplinervia Mart. in Flora 24 (2 Beibl.):67. 1841.
Ficus arpazusa Casaretto, Nov. Stirp. Bras. 15. 1842.
Ficus cerasifolia Kunth & Bouché, Ind. Sem. Hort. Berol. 16. 1846.
Ficus planicostata Kunth & Bouché, loc. cit. 1846.
Ficus periplocaefolia Kunth & Bouché, loc. cit. 1846.
Ficus consanguinea Kunth & Bouché, loc. cit. 1846.
Urostigma erythrostictum Miquel, in Hooker, Lond. Journ. Bot. 6:540. 1847.
Urostigma geminum Ruiz ex Miquel, in Hooker, Lond. Journ. Bot. 6:547. 1847.
Urostigma scheideanum Miquel, in Hooker, Lond. Journ Bot. 6:539. 1847.
Pharmacosycea peruviana Miquel in Hooker, Lond. Journ. Bot. 7:72. 1848.
Urostigma baccatum Liebm. in Kong. Danske Vidensk. Selsk. Skr. 5 ser. 2:327. 1851.
Urostigma sapidum Liebm. in Kong. Danske Vidensk. Selsk. Skr. 5 ser. 9:327. 1851.
Urostigma turbinatum Liebm. in Kong. Danske Vidensk. Selsk. Skr. 5 ser. 9:327. 1851.
Urostigma sulcipes Miq. in Vers. Med. Akad. Amsterdam, 13:413. 1862.
Ficus ochroleuca Griseb. Fl. Brit. W. Ind. Isl. 151. 1864.
Ficus faydeni Miq. Ann. Mus. Bot. Lugd.-Bat. 3:219. 1867.
Ficus baccata (Liebm.) Miq. loc. cit. 3:299. 1867.
Ficus erythrosticta (Miq.) Miq. loc. cit. 3:298. 1867.
Ficus liebmanniana Miq. loc. cit. 1867.
Ficus gemina (Ruiz, ex Miq.) Miq. loc. cit. 1867.
Ficus sapida (Liebm.) Miq. loc. cit. 1867.
Ficus sulcipes (Miq.) Miq. loc. cit. 1867.
Ficus turbinata (Liebm.) Miq. loc. cit. 1867.
Ficus fasciculata S. Wats. in Proc. Amer. Acad. 24:78. 1889, non King (1888).
Ficus sonorae S. Wats. loc. cit. 1889.
Ficus immersa Warb. in Bull. Soc. Bot. Fr. 59 (Mem. 3):641. 1912. (1913), nom. nud.
Ficus palmicida Pittier, in Bol. Soc. Venez. Cienc. Nat. 4^{30}:69. 1937.
Ficus peruviana (Miq.) Rossb. in Fedde, Repert. 43:61. 1937.
Ficus kanukuensis Standl. in Lloydia. 2:174. 1939.
Ficus tarapotina Warburg, mss.

Large spreading trees to 30 m. or more tall. Twigs 1–2 mm. in diameter, glabrous, or pubescent, developing a yellowish grey periderm. Stipules 5–7 mm. long, narrowly deltoid, glabrous or minutely puberulent. Lamina 1–5 cm. wide × 2.5–12 cm. long, elliptic or lanceolate; apex bluntly acute, acute or acuminate, the acumen 5–20 mm. long; base commonly cuneate, sometimes rounded cuneate, seldom rounded and slightly emarginate; lateral veins (4–) 6–12, departing from the midrib at an angle from 20°-60°; intercostals somewhat raised. Petiole 5–30 mm. long, $\frac{1}{5}$–$\frac{1}{8}$ (–$\frac{1}{12}$) as long as the lamina. Figs 5–18 mm. in diameter, globose, glabrous, borne among the leaves; color pink or yellow or green with brown flecks; peduncle 2–5 mm. long, glabrous; basal bracts 1–4 mm. long, semicircular, glabrous; ostiole 1–2 mm. in diameter, crateriform, the bracts sunken into the receptacle or surrounded by a raised ring of receptacular tissue.

Southern Mexico and Jamaica to Paraguay. In lowland to highland forests and savannas. *Mata palo, higuito.*

BOCAS DEL TORO: Changuinola Valley, *Dunlap 350.* CANAL ZONE: Barro Colorado Island, *Aviles 47, Salvoza 910, Bangham 444.* CHIRIQUÍ: Boquete, *Davidson 652, Pittier 2889.*

This, and *Ficus citrifolia* are undoubtedly the most widespread of the American species of the genus. This species, which is immediately recognized by its peculiar crateriform ostiole and narrowly lanceolate or elliptic leaves, differs from *F. citrifolia* in being absent from all of the West Indies except Jamaica, and being very common in Mexico and Central America (The Jamaican population is obviously related to the Central American!). There is a very definite distinction between populations on the basis of fruit size, but there is no sharp discontinuity either in measurements or in geography. In general, however, it can be said that the populations on the Caribbean coast of South America from Venezuela east to the Amazon, and in the Amazon basin, are relatively small fruited, while the Jamaican, Mexican, Central American, and southern and central Brazilian populations are relatively large fruited. With a few exceptions, in the island of Jamaica, the Brazilian population has larger figs than the Central American. This seems to me a peculiar, and probably quite significant pattern of distribution, but of what, or how, I cannot say. It goes without saying that an intensive study of this species in the field should be most rewarding.

The synonymy of this species is extensive but relatively simple. The name *Ficus pertusa* is based on a specimen from Surinam which represents the small fruited populations of that area. *F. subtriplinervia, F. erythrosticta, F. gemina, F. tarapotina* and *F. kanukuensis* all refer to this same general population. *F. padifolia* is the earliest name for the relatively large fruited populations in Colombia, Central America, Mexico and Jamaica. *F. complicata, F. lancifolia, F. ochroleuca, F. faydeni, F. baccata, F. sulcipes, F. sapida* and *F. turbinata* all refer to the same general population. *Ficus arpazusa* is the earliest name for the plants of south Brazilian and eastern Peruvian regions, which Warburg called *F. immersa.*

10. FICUS TRACHELOSYCE Dugand, in Caldasia 4:69. *fig. 14.* 1942.

Strangler trees to about 25 m. tall, the young branches slender, glabrous, developing a thin yellowish periderm. Leaves oblong-elliptic, narrowly subcaudate-acuminate, broadly obtuse at the base, 6–12 cm. long, 2.5–5.0 cm. broad, rather closely pinnate-veined, submembranaceous, glabrous, the petiole 1.5–2.0 cm. long, slender; stipules narrowly lanceolate, subcoriaceous, about 1.5 cm. long. Receptacles paired at the nodes, subglobose, about 15 mm. broad, glabrous, the osteole

Fig. 55. *Ficus trachelosyce*

depressed within a conspicuously elevated collar about 5 mm. long; involucral bracts 2, minutely deltoid, scarcely 1 mm. long; peduncle rather slender, about 5 mm. long.

Panama and Colombia, probably also in southwestern Costa Rica, in lowland forests.

CHIRIQUÍ: Puerto Armuelles, *Allen 6295*.

The above description was prepared by Dr. Woodson. I strongly suspect that this is simply a form of *Ficus pertusa.*

11. FICUS BULLENEI I. M. Johnston, in Sargentia 8:113. 1946.

Trees to 21 m. tall; twigs 3–4 mm. in diameter, frequently conspicuously angled, densely spreading reddish-brown pubescent, eventually developing a rather thick grey periderm; stipules 10–20 mm. long, deltoid, densely appressed, reddish-brown pubescent; lamina 45–110 mm. wide × 100–200 mm. long, oblong-obovate to broadly obovate or oval, densely spreading pubescent, especially below, becoming glabrate above; apex rounded, acute, or minutely acuminate; base rounded, rounded cuneate, or cuneate, sometimes emarginate; lateral veins 4–8 pairs, departing from the midrib at an angle of 20°–40°; basal veins departing from the midrib at a similar angle or from 40°–60°; intercostals not prominent; petiole 10–30 mm. long, $\frac{1}{6}$–$\frac{1}{10}$ the length of the lamina. Figs about 15 mm. in diameter, globose, minutely and densely spreading pubescent, borne among the leaves; color not noted; peduncle 1–4 mm. long; basal bracts two, 4–5 mm. long, ovate-deltoid; orifice about 2 mm. in diameter, surrounded by a raised collar of receptacular tissue, 2–3 mm. high.

Panama, in lowland forests and savannas.

CANAL ZONE: Corozal, *Allen 1837*. PANAMÁ: San José Island, *Johnston 231, 389, 643, 723, 805, 1367, Erlanson 136*.

12. FICUS CITRIFOLIA P. Mill. Gard. Dict. ed. 8. *Ficus* no. 10. 1768.

Ficus pedunculata Dryand. in Ait. Hort. Kew. ed. 1. 3:450. 1789.
Ficus populifolia Desf. Tabl. ed. 1. 239. 1804, nom. nud. (fide herb. Desf.).
Ficus populnea Willd. Sp. Pl. ed. 4. 4:1141. 1806.
Ficus laevigata Vahl, Enum. 2:183. 1806.
Ficus lentiginosa Vahl, loc. cit. 1806.
Ficus gigantea HBK. Nov. Gen. & Spec. 2:48. 1817.
Ficus rubrinervis Link, Enum. Pl. Hort. Berol. 2:448. 1822.
Ficus eximia Schott, ex Spreng. Syst. Veg. ed. 16. 4 (App.): 410. 1827.
Ficus pyrifolia Desf. Cat. Hort. Par. ed. 3. 413. 1829.
Ficus catesbaei Steud. Nomencl. ed. 2. 1:636. 1840.
Ficus botryapioides Kunth & Bouché, Ind. Sem. Hort. Berol. 15. 1846.
Ficus syringaefolia Kunth & Bouché, loc. cit. 1846.
Urostigma angustifolium Miq. in Hook. Lond. Journ. Bot. 6:539. 1847.
Urostigma amazonicum Miq. loc. cit. 541. 1847
Ficus brevifolia Nutt. Sylva, ed. 1. 2:3. 1854.
Ficus surinamensis Miq. Ann. Mus. Bot. Lugd.-Bat. 3:219. 1867.
Ficus angustifolia (Miq.) Miq. loc. cit. 298. 1867, nec Blume (1826) nec Roxb. (1814).
Ficus amazonica (Miq.) Miq. loc. cit. 1867.
Ficus thomaea Miq. loc. cit. 299. 1867.
Ficus populoides Warb. in Urb. Symbol. Antill. 3:479. 1903.
Ficus rectinervis Warb. in Bull. Soc. Bot. France 59 (Mem. 3):642. 1912 (1913), nom. nud.

Ficus brittonii Boldingh, Fl. Curaçao 20. 1914.
Ficus hemsleyana Standl. in Contrib. U. S. Nat. Herb. 20:29. 1917 (non King, 1887).
Ficus guaranitica Chodat, in Bull. Soc. Bot. Genève. 2 ser. 11:254. 1919 (1920).
Ficus turbinata Pitt. in Bol. Soc. Venez. Cienc. Nat. 4^{30}:61. 1937 (non Willd. 1806).
Ficus subandina Dugand, in Caldasia 1^{4}:66. 1942.
Ficus standleyana Dugand, loc. cit. 2:441. 1944.
Ficus antimanensis Pitt. Mss.
Ficus dugandii auct.

Trees to 16 m. tall, or in exposed places, a shrub 0.3–2 m. tall. Twigs 2–6 mm. in diameter, glabrous, with a thin yellowish periderm. Stipules 5–30 mm. long, narrowly deltoid, glabrous, sometimes somewhat glaucous. Lamina 1.5–12 cm. wide × 2.5–20 cm. long, lanceolate, ovate, elliptic, elliptic-lanceolate, elliptic-ovate, oblong, or obovate; apex acute to acuminate; base rounded, rounded-cuneate cuneate, or truncate, frequently emarginate or subcordate; lateral veins 4–16 pairs, departing from the midrib at an angle from 10°–40°; basal veins, departing from the midrib at a similar angle, or to 60°; intercostals not, or scarcely, prominent. Petiole 7–70 mm. long, slender, ½–⅐ (–⅛) the length of the lamina. Figs 6–12 [–15] mm. in diameter, globose, glabrous, borne among the leaves; color reddish or yellowish when ripe; peduncle 2–18 mm. long, glabrous or puberulent; basal bracts two, 2–3 mm. long, broadly deltoid to semicircular, with a hyaline margin, glabrous or puberulent; orifice 2–3 mm. in diameter, flat or very slightly raised.

Florida to Paraguay, in lowland forests.

CANAL ZONE: Chagres, *Fendler 286*; Limón Bay, *Johnston 1533, 1548*; Culebra, *Pittier 2318*; Balboa, *Standley 25473, 25580*; Barro Colorado Island, *Standley 41129*. PANAMÁ: San José Island, *Johnston 109, 494, 680, 752, 1063, 1077, 1109, 1168, 1177, 1381, 1387, 1389, 1390*; Taboga Island, *Standley 27887*.

F. hemsleyana Standl. Standley published this name as a substitute for the epithet *verrucosa* of Liebmann. Standley apparently did not see the type, for the material that he has cited which I have seen (*Tonduz 11576; Fendler 286*) represents a form of *F. citrifolia.* Oersted's plant is a very different thing, perhaps allied to *F. petiolaris* or *F. obtusifolia.*

Ficus citrifolia, as I understand it, is a species which ranges from Florida to Paraguay. Though there seems to be little direct evidence, I presume that this is frequently a species of disturbed habitats. Specimens from relatively high altitudes (600–1700 m.) in the Greater Antilles and Venezuela and Colombia (*F. populoides, F. turbinata, F. subandina*) may represent a separate taxon, though present information suggests that they are only ecological forms. There is not enough information at present to evaluate their status.

The leaf shape is generally ovate, with the base rounded and/or more or less emarginate. The leaf bases may vary from round to emarginate on the same twig. Along the northern coast of South America and the eastern coast of Central America, from the Guianas to Honduras, the leaf form seems to be predominantly oblong (*F. angustifolia, F. surinamensis, F. hemsleyana, F. standleyana*). Forms occur, however, which are transitional to the normal leaf form of the species.

The type of *Ficus citrifolia* is in the Banksian Herbarium at the British Museum (NH). It consists of a twig with two leaves and a peduncle with the remnants of a fig. There is no doubt that it represents this common lowland fig of the West Indies. The Catesby plant to which Miller makes reference is not a particularly good representation, but N. L. Britton refers to it here.

13. Ficus trigonata L. Pl. Surinam. 17. 1775.

Ficus crassinervia Desf. ex Willd. Sp. Pl. ed. 4. 4:1138. 1806.
Ficus berteroi Warb. in Urb. Symbol. Antill. 3:468. 1903.
Ficus eggersii Warb. loc. cit. 469. 1903.
Ficus mamillifera Warb. loc. cit. 470. 1903.
Ficus stahlii Warb. loc. cit. 1903.
Ficus hartii Warb. loc. cit. 458. 1903.
Ficus coombsii Warb. loc. cit. 456. 1903.
Ficus mitrophora Warb. loc. cit. 457. 1903.
Ficus yucatanensis Standl. in Cont. U. S. Nat. Herb. 20:33. 1917.
Ficus pittieri Standl. loc. cit. 31. 1917, pro parte, quoad paratypus.
Ficus campbellii I. M. Johnston, in Sargentia 8:114. 1949.
Ficus leavensii I. M. Johnston, loc. cit. 117. 1949.
Ficus fawcettii Britton, Mss.

Large, spreading trees, to 15–25 m. tall. Twigs 2–5 mm. in diameter, glabrous or pubescent, developing a greyish-yellow periderm; stipules 15–27 mm. long, deltoid, glabrous or pubescent. Lamina 3–12 cm. wide × 4.5–25 cm. long, elliptic, or generally somewhat obovate; apex sometimes acute or even slightly acuminate, but generally rounded; base cuneate, rounded, or emarginate, sometimes slightly inequilateral; lateral veins (5–) 6–11 pairs, departing from the midrib at an angle from 20°–40°; basal veins 1–2, departing from the midrib at an angle from 30°–50°; intercostals slightly prominent. Petiole 7–50 mm. long, ¼–⅑ the length of the lamina. Figs 10–14 (–30) mm. in diameter, globose, glabrous or pubescent, borne among the leaves; color green when immature, red when mature; peduncle obsolete, or 2–10 mm. long, glabrous or puberulent; basal bracts two, 2–5 mm. long, deltoid or semicircular, sometimes variously split, variously glabrous, ciliolate, or puberulent; orifice 1–3 mm. in diameter, plane or slightly umbonate.

Greater Antilles and the Carribbean coast of Central America from Yucatan to Colombia.

canal zone: Gamboa, *Pittier 2602*; Chagres, *Fendler 285*; south of Fort Sherman, *Johnston 1640*. coclé: El Valle de Antón, *Allen 1981*; Penonomé, *Williams 404*. panamá: San José Island, *Johnston 3, 495, 695, 721, 730, 791, 959, 1012, 1121, 1125, 1127, 1353, 1384*; *Erlanson 106, 206*; *Miller 1910*.

This is apparently one of the common figs of the Greater Antilles. While there is considerable vegetative variation within the species, there seems to be no discernable geographical restriction of the variation and, consequently, there seems to be little justification in recognizing a distinct species on each island. Besides this, it seems to be fairly common in Central America.

I have not seen all of the material cited by Standley under the name *Ficus velutina*, but the Panama collection (*Pittier 3359*) is surely this species.

14. Ficus paraensis (Miq.) Miq. in Ann. Mus. Bot. Lugd.-Bat. 3:298. 1867.

Urostigma paraensis Miq. in Hook. Lond. Journ. Bot. 6:534. 1847.
Ficus myrmecophila Warb. in Karsten & Schenck, Vegetationsbilder 3: *t. 2* et sub *t. 3–4.* 1905.
Ficus panamensis Standl. in Contrib. U. S. Nat. Herb. 20:15. 1917.
Ficus thelephora Benoist, in Arch. Bot. (Caen) Bull. 3:171. 1929 (1931).
Ficus haughtii Standl. in Publ. Bot. Field Mus. Nat. Hist. 17:170. 1937.
Ficus uberrima Standl. loc. cit. 177. 1937.
Ficus putumayonis Dugand, in Caldasia 1^4:62. 1942.
Ficus arukensis Standl. in Bull. Torr. Bot. Club 75:295. 1948.
Ficus manabiensis Standl. Mss.

Shrubs, or small to large trees to 10 m. tall. Twigs 2–7 mm. in diameter, glabrous or minutely puberulent, developing a greyish-brown, striate, periderm. Stipules to 35 mm. long, narrowly deltoid, glabrous or minutely puberulent. Lamina 2.5–9 cm. wide × 6–27 cm. long, oblong, oblong-elliptic, oblong-oblanceolate or oblanceolate, glabrous; apex acuminate, the acumen commonly 5–10 mm. long, but sometimes to 25 mm.; base cordate, emarginate, rounded, or cuneate; lateral veins 9–18 pairs, departing from the midrib at an angle from 10°–30°; basal veins, at least the strongest, departing from the midrib at an angle from 40°–60°; intercostals scarcely, or somewhat, prominent. Petiole 5–35 (–80) mm. long, ⅓–⅑ (–1⁄11) the length of the lamina. Figs 10–18 mm. in diameter, globose to sub-pyriform, glabrous or minutely puberulent, borne among the leaves; color greenish or yellowish, sometimes with red streaks and sometimes with crimson basal bracts; peduncle obsolete to 3 mm. long; basal bracts 2–5 mm. long, ovate, connate, puberulent; ostiole 2–4 mm. in diameter, umbonate, to 3 mm. high.

Southern Mexico to Peru and northern Brazil, in lowland forests.

canal zone: Barro Colorado Island, *Bailey & Bailey 23*; Madden Road, *Allen 2540*. colón: Río Fató, *Pittier 3893, 3908*. panamá: San José Island, *Johnston 627, 251, 1134, 1174 1365, 1409.*

The ripe receptacles appear to be olive green with purplish stripes and prominent purplish osteoles. Johnston (in Sargentia 8:118–119, 1949, *sub F. panamensis*), notes that although a strangler, *F. paraensis* does not appear to kill its host tree.

As here understood, *Ficus paraensis* is a common and widespread species in the lowland rainforest, ranging from southern Mexico (fide Standley) along the Caribbean coast to Panama, thence along the western coast of South America at least as far as Ecuador, and along the eastern coast of South America to the mouth of the Amazon, and westward from this to the foot of the Andes. There are a good many collections, particularly from Central America and the western part of the Amazon basin, with rather thick (5–7 mm. in diameter) twigs. In these same areas, and on the western coast of South America, forms with strongly emarginate (or cordate) leaf bases are also common. I suspect that these collections represent juvenile plants or shoots. Throughout the area of distribution, mention is made that ants build nests on the stems and branches of plants of this species.

15. Ficus nymphaeaefolia P. Mill. Gard. Dict. ed. 8. *Ficus* no. 9. 1768.

Ficus numphaeifolia L. Mant. Plant. Alt. 305. 1771.
Ficus nymphoides Thunb. Ficus Genus Dissert. 7. 1786.
Ficus ierensis Britton, in Bull. Torr. Bot. Club 48:329. 1921.
Ficus anguina R. Benoist, in Bull. Mus. Hist. Nat. (Paris) 30:104. 1924.
Ficus duquei Dugand, in Caldasia 1[4]:42. 1942.

Trees 7–35 m. tall, glabrous. Twigs 4–13 mm. in diameter, glabrous or minutely puberulent. Stipules to 40 mm. long, lanceolate or deltoid, glabrous or minutely puberulent, or glaucous. Lamina 6.5–20 cm. wide × 9–30 cm. long, ovate or ovate-rotund; apex acute, broadly acute, rounded, or sometimes shortly acuminate; base cordate; lateral veins (4–) 5–11 pairs, departing from the midrib at an angle from 10°–40°; basal veins departing from the midrib at an angle of 20° or less; intercostals not prominent. Petiole 30–200 mm. long, ½–¼ the length of the lamina. Figs 15–25 mm. in diameter, globose, minutely puberulent or glaucous, borne among the leaves; color greenish, with purple spots; peduncle obsolete to 5 mm. long; basal bracts 4–19 mm. long, deltoid or ovate, connate, minutely puberulent or glaucous; ostiole 2–3 mm. in diameter, probably plane with the surface, but in dried material frequently raised, or surrounded by a more or less distinct ring of receptacular tissue.

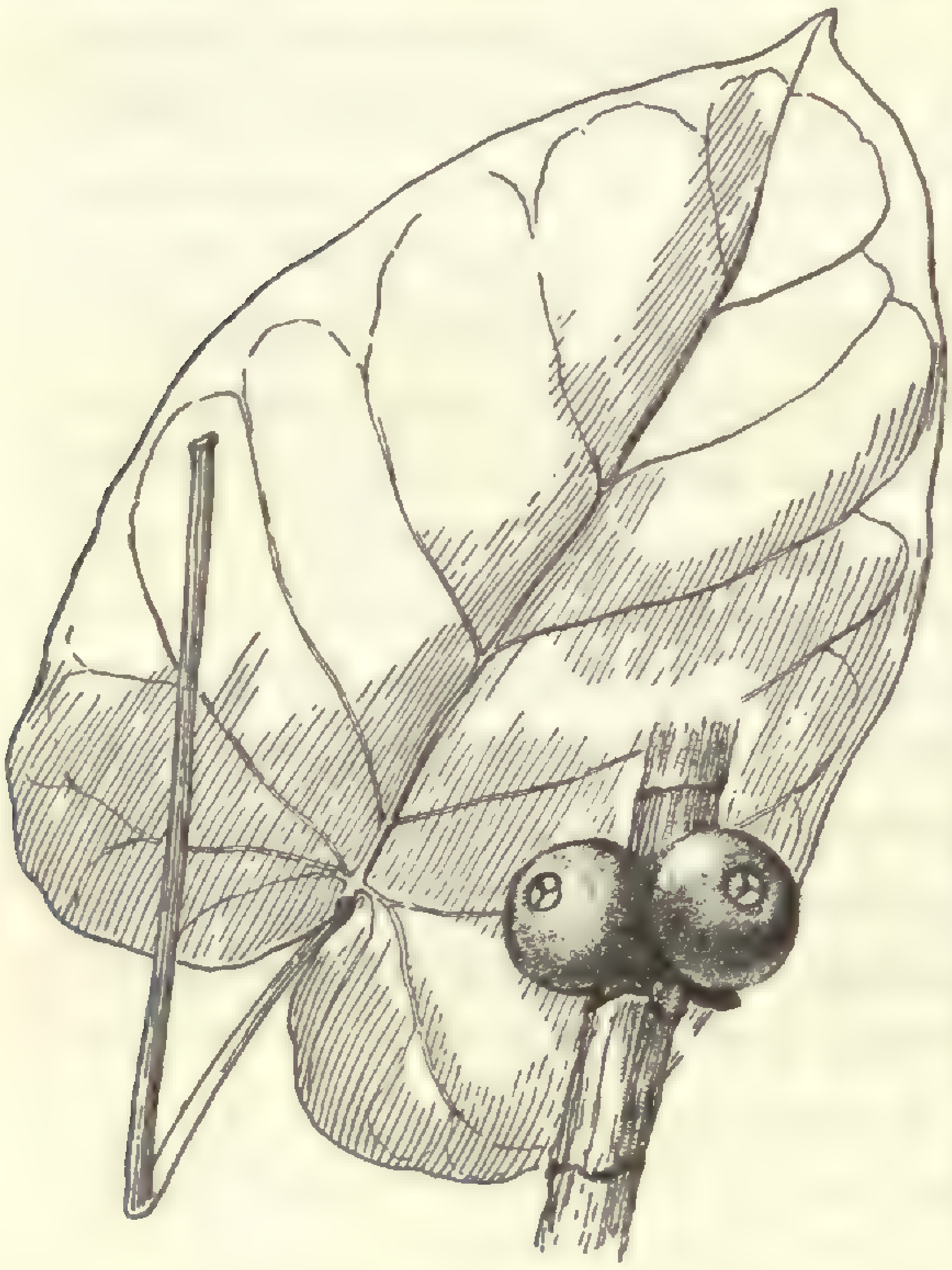

Fig. 56. *Ficus nymphaeaefolia*

Costa Rica to State of Amapa, Brazil, in lowland forests.

CANAL ZONE: northwestern part of Canal Zone, *Johnston 1596*; Maru Towers, *Johnston 1550*; Barro Colorado Island, *Shattuck 267, Woodworth & Vestal 708, 392, Bailey & Bailey 373*; Madden Reservoir, *Muenscher 12299*.

This seems to be a fairly common species on the lower slopes (below 1000 m.) of the mountains behind the coast, and in the lowland forests, from Panama to the mouth of the Amazon. Humboldt found it in the coastal mountains of Venezuela and recorded it as having many buttress-like aerial roots. The species seems to be quite uniform throughout its range, though there are a few minor variations. The few specimens I have seen from Panama have the apex of the leaf very shortly acuminate. Some of the Colombian material and specimens from Trinidad have larger basal bracts to the fig than are found in material from other areas, but the Trinidad material differs from the Colombian in that it seems not to have tabular crystal cells in the veins.

16. FICUS OBTUSIFOLIA HBK. Nov. Gen. & Sp. 2:49. 1817, non Roxb. (1814).

Urostigma involutum Liebm. in K. Dansk. Vid. Selsk. Skrivt. 5 ser. 2:320. 1851.
Urostigma bonplandianum Liebm. loc. cit. 323. 1851.
Ficus involuta (Liebm.) Miq. in Ann. Mus. Bot. Lugd.-Bat. 3:298. 1867.
Ficus bonplandiana (Liebm.) Miq. loc. cit. 1867.
Ficus proctor-cooperi Standl. in Field Mus. Publ. Bot. 4:201. 1929.

Trees to about 20 m. tall. Twigs 5–6 mm. in diameter, glabrous or pubescent, with thick wrinkled grey periderm. Stipules to 30 mm. long, deltoid, glabrous. Lamina 3.5–12 cm. wide × 9–25 cm. long, oblanceolate to broadly obovate, glabrous; apex rounded or bluntly acute; base cuneate; lateral veins 5–11 pairs, departing from the midrib at an angle from 20°–40°; basal veins departing from the midrib at an angle from 40°–50°; intercostals not, or scarcely, prominent. Petiole 10–30 mm. long, ⅙–⅑ the length of the lamina. Figs 15–20 mm. in diameter, globose, glabrous or minutely puberulent, borne among the leaves; color not noted; peduncle obsolete to 8 mm. long, puberulent; basal bracts two, 4–7 mm. long, semicircular, connate, sometimes more or less split, finely pubescent; orifice 3–5 mm. in diameter, flat or somewhat umbonate.

Southern Mexico to northern Peru, in lowland forests.

CANAL ZONE: Daytonia Farm, *Cooper 436*; Gamboa, *Standley 28524*; Fort Randolph, *Standley 28729*; Barro Colorado Island, *Woodworth & Vestal 619, Kenoyer 320*. SAN BLAS: Permé, *Cooper 641*.

This is apparently a fairly widespread species, ranging from Central Mexico to northern Guatemala, thence along the Pacific Coast through Costa Rica and Colombia to northern Peru. It ranges in altitude from near sea level to 1500–1800 m.

I have seen the HBK. type in Paris and the Liebmann types from Copenhagen. There can be no question but that these are conspecific.

The name *Ficus obtusifolia* was first used by Roxburgh in the Hortus Bengalensis in 1814. It was here a nomen nudum, not validly published, so that it does not invalidate the publication of *Ficus obtusifolia,* HBK. in 1817. Roxburgh's name was not validly published until 1832.

I have not seen the type of *Ficus proctor-cooperi* Standley. That name is included in synonymy here on the authority of Dr. Woodson.

17. FICUS COSTARICANA (Liebm.) Miq. in Ann. Mus. Bot. Ludg.-Bat. 3:298. 1867.

Urostigma costaricanum Liebm. in K. Dansk. Vid. Selsk. Skrivt. 5 ser. 2:322. 1851.
Ficus kellermannii Standl. in Contrib. U. S. Nat. Herb. 20:18. 1917.

Trees 12–15 m. tall. Twigs 3–5 mm. in diameter, pubescent or glabrate, developing a rather thin brownish grey periderm. Stipules 12–25 mm. long, broadly deltoid, glabrous, persistent. Lamina 3–7.5 cm. wide × 6–18 cm. long, oblanceolate or oblong-elliptic, frequently somewhat inequilateral, glabrous; apex rounded, acute, or shortly blunt acuminate; base rounded or rounded cuneate, emarginate; lateral veins 5–12 pairs, departing from the midrib at an angle from

Fig. 57. *Ficus costaricana*

20°–30°; basal vains departing from the midrib at an angle of 50°–60°; intercostals prominent. Petiole 5–30 mm., 1/6–1/9 the length of the lamina. Figs 10–12 mm. in diameter, depressed globose; glabrous, borne among the leaves; color reddish with darker spots; peduncle obsolete; basal bracts 5–10 mm. broadly deltoid, glabrous.

Guatemala to Panama, at low or intermediate elevations.

CANAL ZONE: Barro Colorado Island, *Woodworth & Vestal 572, Salvoza 937, Standley 41148*. CHIRIQUÍ: David, *Pittier 2826, 2835*; Caldera, *Pittier 3348*.

The persistent stipules and the oblate reddish receptacles with rather thin flesh are outstanding traits of this species. It also is represented by S. *Hayes 838* (*sine loco*).

18. FICUS TUERCKHEIMII Standl. in Contrib. U. S. Nat. Herb. 20:13. 1917.

Ficus isophlebia Standl. loc. cit. 14. 1917.
Ficus jimenesii Standl. loc. cit. 1917.

Trees to 30 m. tall. Twigs 4–6 mm. in diameter with crowded internodes, glabrous, developing a rather thick reddish-brown periderm. Stipules 15–20 mm. long, narrowly deltoid, glabrous, sometimes glaucous. Lamina 3–10.5 cm. wide × 4–17 cm. long, broadly oval or ovate, glabrous; apex rounded or bluntly acute; base rounded cuneate, rounded, truncate, sometimes more or less emarginate or subcordate; lateral veins 7–10 pairs, departing from the midrib at an angle from (15°–) 25°–40°; basal veins departing from the midrib at a similar angle or up to 70°; intercostals not prominent. Petiole 20–65 mm. long, 2–3 mm. thick, 1/2–

⅓ (–⅕) the length of the lamina. Figs 9–14 mm. in diameter, depressed globose, glabrous, borne among the leaves; color not noted; peduncle obsolete; basal bracts 10–15 mm. long, rounded deltoid, surrounding the receptacle and adherent to it for about 5 mm.

British Honduras to Panama and possibly southward, in lowland forests.

BOCAS DEL TORO: Puerto Armuelles, *Woodson & Schery, 812.* CHIRIQUÍ: David, *Pittier 2821.*

Possibly more than one species is represented here, but I doubt it. The receptacles are so closely sessile as a rule that the growing twig beneath them develops curious persistent sockets which remain long after the fruit has fallen.

19. FICUS DAVIDSONIAE Standl. in Field Mus. Publ. Bot. 22:15. 1940.

Trees to 30 m. tall. Twigs stout, glabrous, with a thick brown periderm. Stipules about 10 mm. long, deltoid. Lamina 4–7 cm. wide × 8–15 cm. long, oblanceolate or broadly obovate, glabrous; apex rounded or obtuse; base cuneate or broadly cuneate; lateral veins 8–12, departing from the midrib at an angle of 20°–30°; basal veins departing from the midrib at an angle of 50°–60°; intercostals not prominent. Petiole 10–20 mm. long, ⅛ the length of the lamina. Figs 8–10 mm. in diameter, globose, glabrous, borne among the leaves; color unknown; peduncle obsolete; basal bracts broadly rounded, deltoid, about as long as the receptacle.

El Salvador to Panama, in higher-elevation forests.

CHIRIQUÍ: Boquete, *Davidson 534, 688; Von Hagen & Van Hagen 2095.* COCLÉ: La Mesa, *Allen 2832.*

For this species I have seen only a leaf of *Davidson 688.* On the basis of general shape and proportions, confirmed by the structure of the lower epidermis, this seems to be fairly closely related to *Ficus clusiaefolia* Schott, ex Spreng. of the eastern coast of South America from Venezuela to Rio de Janiero.

13. POUROUMA Aubl.

POUROUMA Aubl. Hist. Pl. Guian. Fr. 2:891. 1775.

Puruma St.-Hil. Expos. Fam. 2:313. 1805, var. orth.

Dioecious trees, frequently epiphytic and strangling when juvenile, the branches usually stout and hollow. Leaves spiral, basifixed, entire to deeply lobed; stipules fully amplexicaul and leaving a scar completely surrounding the stem. Inflorescences repeatedly cymose, the flowers rather indefinitely glomerate at the ends of the branches. Staminate flowers with 4 nearly free tepals and 4 free stamens. Pistillate flowers with a fleshy cupular or tubular perianth, epigynous; stigma obscurely 2-lobed. Fruit a somewhat fleshy false drupe of moderate size.

Perhaps 30 or more species from southern Mexico to Bolivia and Brazil. In Panama and Costa Rica the trees are known locally as *guarumo,* a name applied to certain other quite unrelated plants with a milky or mucilaginous sap.

The species of *Pourouma* are perhaps the most ambiguous and vexatious of American Moraceae, a dubious distinction. The representation from Panama is extremely meagre and very little, if anything, is known of the variability of the species of the genus in any part of its range. The flowers apparently display little in the way of systematic variation. Consequently the species which follow are quite tentative.

a. Leaves not deeply lobed, the median lobe divided about halfway or less to the petiole and scarcely constricted at the base (sometimes entire or subentire in *P. radula*).
  b. Pubescence spreading fulvous-tomentellous; leaves 3-lobed or sometimes entire. .... 1. P. RADULA
  bb. Pubescence rubiginous-papillate, variously interspersed-hispid; leaves usually 5-lobed. .... 2. P. JOHNSTONII
aa. Leaves deeply lobed, the median lobe divided about two-thirds or more to the petiole, definitely constricted at the base.
  b. Pubescence (except the upper inflorescence) appressed-sericeous; leaves usually 3-lobed .... 3. P. SCOBINA
  bb. Pubescence rubiginous-papillate, variously interspersed-hispid; leaves usually 7- to 9-lobed .... 4. P. ORARIA

1. POUROUMA RADULA R. Bén. in Bull. Mus. Hist. Nat. Paris 28:320. 1922.

Trees of moderate size, the young branches relatively slender, minutely fulvous-tomentellous to glabrate. Leaves variable, entire and ovate-elliptic to broadly 3-lobed with the median lobe divided about halfway to the petiole and scarcely constricted at the base, obtuse to broadly acute at the tip, rounded to cordate at the base, 10–25 cm. long and 6–15 cm. broad, firmly membranaceous, scabridulous above, densely and minutely fulvous-tomentellous beneath, the petiole 2–12 cm. long, rather slender, densely and minutely fulvous-tomentellous. Inflorescences about as long as the subtending petioles or somewhat shorter, densely and minutely fulvous-tomentellous. Fruits broadly ovoid, about 1.5 cm. long, minutely fulvous-tomentellous.

Panama to the Guianas, in lowland forests.

"PANAMA": locality unknown, *Hayes 860*.

The leaves of this specimen coincide fairly well with those of the type specimen of *P. aspera* Tréc., tracings of which were sent me by M. Léandri of Paris. However Trécul describes the pubescence of *P. aspera* as consisting of "*pilis albis adpressis*".

2. POUROUMA **johnstonii** Woodson, spec. nov.

Arbores ut dicitur ca. 7–12 m. attingentes, ramulis crassis fistulosis dense rubiginoso-papillatis pilis hispidis interspersis. Folia latissime 5–lobata basi amplectante cordata supra scaberula subtus pallidiora inter venas venulasque hirtellas minute appresse arachnoideo-villosula, lobis breviter acuminatis per longetudinem ca. dimidiam basi conjunctis parte libra medii ca. 20 cm. longa 15 cm. lata, 2 exteriorum ca. 5 cm. longa et lata sinibus obtusis, petiolis ca. 20 cm. longis minute rubiginoso-papillatis pilis hispidis interspersis; stipulis anguste laceolatis ca. 8–10 cm. longis extus rubiginoso-papillatis pilis hispidis interspersis. Flores sexum

Fig. 58. *Pourouma radula*

amborum ignoti. Pedunculi fructiferi 2 ca. 10–15 cm. longi parte inferiori rubiginoso-papillatis pilis hispidis interspersis, fructibus late compresse ovoideis ca. 1.5 cm. longis 1 cm. latis dense rubiginoso-papillatis.

CANAL ZONE: Maru Towers, west of Limón Bay, March 27, 1956, *I. M. Johnston 1714* (MO, HOLOTYPE); railroad relocation between Gorgona and Gatún, *Pittier 2286*.

Closely related to *P. oraria*, but probably distinct as set forth in the key.

3. POUROUMA SCOBINA R. Bén. in Bull. Mus. Hist. Nat. Paris 28:320. 1922.

Trees to about 30 m. tall, the branches stout, hollow, appressed-sericeous to glabrate. Leaves at maturity deeply 3-lobed, broadly cordate, about 10–25 cm. long and broad, the lobes divided about two-thirds to the petiole, the median lobe definitely constricted at the base, scaberulous above, pale and densely papillate beneath and appressed-sericeous along the veins, the petiole 20–30 cm. long, densely

appressed-sericeous; stipules narrowly lanceolate, about 8–10 cm. long, densely appressed-sericeous. Peduncles paired at the nodes, slightly shorter than the subtending petioles, densely appressed-sericeous below, rubiginous-papillate above. Neither staminate nor pistillate flowers known from Panama. Fruits broadly compressed-ovoid, about 1.5 cm. long and 1 cm. broad, minutely puberulent.

Guatemala to the Guianas, in forests of intermediate elevations.

COCLÉ: north of El Valle de Antón, *Allen 3742*. DARIÉN: Cana, *Williams 983*.

Closely related to *P. palmata* Poeppig & Endl., in which the leaf base is typically truncate.

4. POUROUMA ORARIA Standl. & Cuatr. in Caldasia 7:301. 1956.

Apparently trees of moderate size, the young branches stout and hollow, densely rubiginous-papillate interspersed-hispid to glabrate. Leaves at maturity deeply 7- to 9-lobed about two-thirds or more to the petiole, deeply amplectant-cordate at the base, about 25–35 cm. long and broad, the median lobe strongly contracted at the base, scaberulous above, paler and densely arachnoid-vilosulose beneath, the petiole about 15–25 cm. long, densely rubiginous-papillate sparsely interspersed-hispidulous; stipules oblong, 8–10 cm. long, densely rubiginous-pulverulent interspersed hispid. Peduncles paired at the nodes, the peduncle somewhat shorter than the subtending petiole, rubiginous-papillate sparsely interspersed-hispidulous. Staminate flowers unknown. Fruits compressed-ovoid, about 1.5 cm. long and 1 cm. broad, densely rubiginous-papillate interspersed-hispidulous.

Panama and Colombia.

"PANAMA": *Hayes 348, 862*.

Reminiscent of *P. cecropiaefolia* Mart. ex Miq. of the Amazon basin, but the leaf lobes are not as deeply divided nor as many as in that species. *Shattuck 260* from Barro Colorado Island may represent a juvenile leaf form.

14. COUSSAPOA Aubl.

COUSSAPOA Aubl. Hist. Pl. Guian. Fr. 2:955. 1775.

Dioecious trees, usually epiphytic when juvenile. Leaves spiral, basifixed, entire to more or less definitely undulate or crenate; stipules fully amplexicaul, leaving a scar completely surrounding the stem. Inflorescences usually paired at the nodes, the staminate dichotomously compounded small globular heads, the pistillate superficially simple or (in *C. magnifolia*) obscurely compound heads. Staminate flowers with 4 (–3) free tepals and 2 completely fused stamens. Pistillate flowers tubular or clavate, the limb thickened and calyptriform and minutely porous much as in *Cecropia,* the ovary superior, with a barely exserted penicillate stigma. Fruit a scantily fleshy syncarp.

About 30 species ranging from southern Mexico to Brazil and Peru. *Coussapoa* resembles *Ficus* in its frequently epiphytic germination and strangling habit, but it is less aggressive in the latter trait. The hollow branches frequently are inhabited by ants.

a. Leaves more or less deeply cordate, the venation subpalmate, with 6–8 pairs of upper secondaries, the tertiaries prominently dendroid and forming a coarse and irregular reticulum; pistillate heads obscurely compound, 2- to 4-lobed. .... 1. C. MAGNIFOLIA
aa. Leaves obtuse or rounded at the base, rarely truncate or obscurely cordate, the venation typically and closely pinnate with 10–20 pairs of secondaries, the tertiaries densely parallel and forming a delicate uniform reticulum; pistillate heads apparently simple, spherical.
b. Pistillate heads long-pedunculate; leaves persistently arachnoid-tomentellous beneath. .... 2. C. PANAMENSIS
bb. Pistillate heads subsessile or very shortly pedunculate; leaves nearly glabrate beneath. .... 3. C. BREVIPES

1. COUSSAPOA MAGNIFOLIA Tréc. in Ann. Sci. Nat. 3 ser. 8:98. 1847.

Coussapoa nymphaeifolia Standl. in Proc. Biol. Soc. Wash. 37:50. 1924, as to specimens cited, in part, not as to type.
Coussapoa chagresiana A. D. Hawkes, in Phytologia 3:30. 1948.

Trees to about 10 m. tall, the branches stout and hollow, minutely ferruginous-tomentellous to glabrate. Leaves broadly oval, broadly rounded at the tip, more or less deeply cordate at the base, 15–30 cm. long, 10–25 cm. broad, entire or indefinitely undulate, firmly membranaceous, minutely puberulent to glabrate beneath, the venation subpalmate and rather distant, with 6–8 pairs of upper secondaries, the tertiaries prominently dendroid and forming a coarse and irregular reticulum, the petioles 5–15 cm. long; stipules about 3–5 cm. long, minutely ferruginous-tomentellous. Staminate inflorescences much shorter than the subtending petioles, about 3– to 4–times dichotomous, the heads nearly 1 cm. broad at anthesis. Pistillate inflorescences obscurely compound, the heads 2- to 4-lobed, 4–5 cm. broad at anthesis, the peduncles simple, about 2–3 cm. long.

Panama to Peru, in lowland forests.

CANAL ZONE: Chagres, *Hayes 354*; Fort San Lorenzo, *Allen 5120*; west of Limón Bay, *Johnston 1768*; Barro Colorado Island, *Kenoyer 321*, *Woodworth & Vestal 606*.

Hayes 354, the type of *C. chagresiana*, was cited by Standley following the description of *C. nymphaeifolia*, but the type of the latter from Costa Rica, *Cook & Doyle 157*, has foliage with more typically pinnate, crowded venation and the pistillate heads are quite sessile. The Panamanian plants seem to coincide exactly with a Pavón isotype photographed at Berlin by Dr. J. Francis Macbride.

2. COUSSAPOA PANAMENSIS Pittier, in Contrib. U. S. Nat. Herb. 18:226. 1917.

Trees up to about 30 m. tall, the branches relatively slender, glabrous or essentially so. Leaves ovate, obtuse at the tip, obtuse or rounded, rarely truncate or obscurely cordate at the base, 10–30 cm. long, 7–15 cm. broad, subcoriaceous, entire to somewhat crenate toward the tip, persistently arachnoid-tomentellous and cinereous beneath, the venation closely and typically pinnate with 10–20 pairs of secondaries, the tertiary venation densely parallel and forming a delicate and uniform reticulum, the petioles 2–8 cm. long; stipules 2–6 cm. long, densely and minutely puberulent-papillate. Staminate inflorescences about equaling or much shorter than the subtending petioles, 2- to 4-times dichotomous, the heads about 5

Fig. 59. *Coussapoa panamensis*

mm. broad at anthesis. Pistillate inflorescences apparently simple, the heads about 1 cm. broad at anthesis, the peduncles 2–6 cm. long, minutely puberulent.

Southern Mexico to Panama and probably extending into northern South America, in lowland forests.

BOCAS DEL TORO: Chaguinola Valley, *Dunlap 299*; Río Cricamola, *Woodson, Allen & Seibert 1893, Cooper 538*; Coca Cay, *Von Wedel 2879*; Water Valley, *Von Wedel 1733*. CANAL ZONE: Fort Sherman, *Standley 30924*; Río Medio, *Miller 1718*; Gatún, *Hayes 414, 986, 1008*; Barro Colorado Island, *Standley 41170, Kenoyer 314, Woodworth & Vestal 445, 660*. COLÓN: Río Fató, *Pittier 3892*. PANAMÁ: San José Island, *Johnston 606, 652, Erlanson 240*.

3. COUSSAPOA BREVIPES Pittier, in Contrib. U. S. Nat. Herb. 18:225. 1917.

Epiphytic shrubs, the branches relatively stout, glabrate. Leaves broadly oval, obtuse to rounded at the tip and at the base, crenate, 10–17 cm. long, 6–11 cm. broad, subcoriaceous, inconspicuously arachnoid beneath to nearly glabrate, the venation rather typically and closely pinnate, with about 11 to 14 pairs of secondaries, the tertiary venation densely parallel and forming a delicate uniform reticulum, the petioles 4–6 cm. long; stipules 4–7 cm. long, minutely and densely arachnoid-puberulent. Staminate inflorescences unknown. Pistillate inflorescences apparently simple, subsessile, the heads about 1 cm. broad at anthesis.

Panama in lowland forests. Known only from the type collection.

SAN BLAS: Sperdí, near Puerto Obaldía, *Pittier 4386*.

A puzzling species, possibly present in Colombia also.

15. CECROPIA L.

CECROPIA L. in Loefl. Iter Hisp. 272. 1758, nom. conserv.

Coilotapalus P. Br. Hist. Jam. 111. 1756, nom. rejic.
Ambaiba Adans. Fam. 2:377. 1763.

Dioecious trees, the trunk and branches stout and hollow. Leaves spiral, eccentrically peltate when mature; stipules fully amplexicaul and leaving a scar completely surrounding the stem. Inflorescences of spadicose spikes in digitate clusters. Staminate flowers: perianth tubular with a somewhat thickened porous operculum; stamens 2. Pistillate flowers: perianth tubular with thin shredding walls and a fleshy porous circumscissile operculum, the penicillate stigma barely exserted. Fruit a minute achene.

Possibly in excess of 80 species of tropical America; a genus badly in need of revision as in most Moraceae, the species of which are probably not as difficult to distinguish as has been supposed.

Cecropia is one of the most conspicuous and picturesque trees of moderate size in clearings and thicket areas because of its rapid growth and long-petioled digitate leaves; it is seldom if ever found in established forests. The hollow trunks and branches almost invariably are the homes of myriads of aggressive ants. It is commonly known as *guarumo*, with various modifications.

Young seedlings of *Cecropia* present what may be an interesting instance of juvenile reversion. The first stem leaves of *C. peltata* are subtended by lateral stipules and are undivided although with more or less undulate-serrate margins; next ensue leaves with fully amplexicaul stipules and basifixed blades which are palmately divided into 3 segments as in many species of *Pourouma*. Finally the excentrically peltate mature foliage is attained.

Fig. 60. *Cecropia peltata*

a. Leaves divided about midway to the center or scarcely beyond, the lobes not contracted toward the base or scarcely so; spadices usually shorter than the common peduncle; spathes about 4–6 cm. long shortly before anthesis.

b. Basal pulvinus of petioles minutely ferruginous-velutinous without conspicuous interspersed longer hairs; staminate spadices in pedunculate clusters of 12–30; pistillate spadices in clusters of 4–6, nearly half as long as the common peduncle; spathes densely arachnoid-villous. .... 1. C. PELTATA

bb. Basal pulvinus of petioles with the ferruginous velamen more or less concealed by interspersed dense white longer hairs; staminate spadices in pedunculate clusters of 50–60; pistillate spadices in clusters of 10–12, far shorter than the common peduncle; spathes shortly hirtellous. .... 2. C. LONGIPES

aa. Leaves divided about two-thirds to three-quarters to the center, the lobes conspicuously contracted toward the base; spadices usually longer than the common peduncle; spathes 10–15 cm. long shortly before anthesis.

b. Leaves smooth above; petioles densely arachnoid-villous; pistillate spadices with enlarged subcalyculate pruinose stipes, 8–10 cm. long at anthesis; staminate spadices about 10.......... 3. C. EXIMIA

bb. Leaves scaberulous above; petioles minutely puberulent or hirtellous; pistillate spadices subsessile or with slender stipes.

c. Leaves conspicuously pellucid-maculate; staminate spadices in clusters of 12–15, 5–6 cm. long; pistillate spadices in clusters of 3–4, about 15 cm. long in fruit.......... 4. C. MAXONII

cc. Leaves not pellucid-maculate; staminate spadices in clusters of 3–6, 12–14 cm. long; pistillate spadices in clusters of 3–4, 25–30 cm. long.......... 5. C. OBTUSIFOLIA

1. CECROPIA PELTATA L. Syst. Nat. ed. 10. 1286. 1759.

Cecropia humboldtiana Kl. in Linnaea 20:530. 1847.
Cecropia arachnoidea Pittier, in Contr. U. S. Nat. Herb. 18:226. 1917.
Cecropia asperrima Pittier, loc. cit. 227. 1917.

Trees 6–20 m. tall with stout, seldom-branching trunks, the young branches stout, hispidulous to glabrate. Mature leaves divided about midway to the center or scarcely beyond, scabridulous above, paler and densely arachnoid-villosulose to glabrate beneath, the lobes usually 9–11, not contracted toward the base or scarcely so, obtuse to rounded at the tip, the petioles densely and minutely hirtellous, with a ferruginous-velutinous basal pulvinus; stipules about 6–9 cm. long, hirtellous. Staminate spadices in clusters of 12–30, 3–5 cm. long, about 4 mm. in diameter, with slender hirtellous stipes about 3–5 mm. long, the spathes 4–6 cm. long shortly before anthesis, broadly conic-oblongoid, densely white-arachnoid-villous, the common peduncle 7–10 cm. long after anthesis, slender, minutely hirtellous. Pistillate spadices in clusters of 4–6, at anthesis about 4–5 cm. long and 5 mm. in diameter, in fruit about 5–10 cm. long and 1 cm. in diameter, subsessile or with very inconspicuous stipes, the spathes as in the staminate inflorescences, the common peduncle about 7–8 cm. long at anthesis, somewhat accrescent in fruit.

Southern Mexico to northern South America and in the Greater Antilles, chiefly in clearings and thickets at low elevations.

CANAL ZONE: Frijoles, *Piper 5837*; Gamboa, *Standley 28477*; Matachín, *Pittier 4056*; Culebra, *Pittier 4060*; Tabernilla, *Pittier 3823*; Barro Colorado Island, *Kenoyer 310*, *Seibert 565*. PANAMÁ: San José Island, *Johnston 154, 155, 78, 471*, *Erlanson 233*, *Harlow 87*.

The leaves of this species, as in all Cecropias, vary so greatly in size and are frequently so large that only a very poor impression is imparted by herbarium specimens. In C. *peltata* mature leaves may attain a diameter of nearly one half meter.

2. Cecropia longipes Pittier, in Contr. U. S. Nat. Herb. 18:227. 1917.

Trees to about 10 m. tall with stout seldom-branching trunks, the young branches very stout, densely gray-hispid to glabrate. Mature leaves divided about midway to the center or less, scabridulous above, paler and subarachnoid-puberulent beneath, the lobes 9–13, not contracted toward the base or scarcely so, broadly obtuse to rounded at the tip, the petioles very stout, densely gray-hirtellous, with the ferruginous velamen of the basal pulvinus more or less concealed by interspersed white longer hairs; stipules about 9 cm. long, ferruginous-hirtellous with interspersed longer white hairs. Staminate spadices in clusters of 50–60, 4–12 cm. long and about 2 mm. in diameter, with slender gray-hirtellous stipes about 2 cm. long, the spathes unknown, the common peduncle about 10–12 cm. long, gray-hirtellous after anthesis. Pistillate spadices in clusters of 8–12, at anthesis about 8–9 cm. long and 5 mm. in diameter, in fruit about 10–12 cm. long and 1 cm. thick, very shortly stipitate, the spathes about 5–6 cm. long, gray-hirtellous, the common peduncle 5–6 cm. long, rather irregularly but conspicuously gray-hirtellous, somewhat accrescent in fruit.

Presently known only from Panama, in thickets and secondary forests at low elevations.

canal zone: Tabernilla, *Pittier 3823, 3825*; Madden Dam, *Woodson Allen & Seibert 1312, 1313*; Fort Sherman, *Johnston 1503*; Barro Colorado Island, *Aviles 63, Bailey & Bailey 421*.

The extremely long pendulous pistillate peduncles are most impressive. The mature leaves may attain a diameter of nearly a meter.

3. Cecropia eximia Cuatr. in Rev. Acad. Colomb. Cienc. 6:287. 1945.

Trees to about 10 m. tall with stout seldom-branching trunks, the young branches very stout, shortly hispidulous to glabrate. Mature leaves divided nearly to the center, smooth and when juvenile sparsely arachnoid-villous above, paler and minutely canescent beneath, the lobes about 9, conspicuously contracted toward the base, broadly acute or obtuse at the tip, the petioles very stout, densely arachnoid-villous with the basal pulvinus ferruginous-velutinous; stipules about 6 cm. long, ferruginous-velutinous with inspersed longer canescent hairs. Staminate inflorescences of about 10 spadices 12–15 cm. long with slender basal stipes about 1.5 cm. long, the common peduncle about 15–20 cm. long, arachnoid-villosulose to glabrate. Pistillate spadices in clusters of about 5, at anthesis 8–10 cm. long and about 8 mm. thick, with enlarged subcalyculate pruinose basal stipes about 1 cm. long, the spathes oblongoid, long-apiculate, about 10–12 cm. long and 2–3 cm. thick shortly before anthesis, gray-hirtellous, the common peduncle about 8–10 cm. long, gray-hirtellous.

Costa Rica to Colombia, in lowland thickets and secondary forests.

BOCAS DEL TORO: Almirante Region, *Slater 48*. CANAL ZONE: area west of Limón Bay, etc., *Johnston 1758*.

At one time I suspected that an earlier name for this species might be *C. insignis* Liebm., described very inadequately from San Juan de Nicaragua. In the herbarium at Copenhagen, which is the chief depository of Oersted's collections, there is no specimen labeled as *C. insignis*. However, 5 sheets of *Oersted 5861*, one of which is noted as having been collected at San Juan de Nicaragua, are referable to *C. peltata* L. in the broad sense employed here.

The description of the staminate inflorescence is taken from a Costa Rican specimen collected in the region of Limón. The Panamanian specimens are pistillate, as in the Colombian type. Three leaf specimens from the Canal Zone and deposited in the U. S. National Herbarium, possibly represent juvenile forms of this species: *Piper 5847, 5840*, and *Killip 12173*. It really is something of a crime, or at least a misdemeanor, to collect leaves of *Cecropia* unaccompanied by inflorescences of at least one sex.

4. CECROPIA MAXONII Pittier, in Contrib. U. S. Nat. Herb. 18:228. 1917.

Trees 10–12 m. tall with stout, seldom-branching trunks, the young branches very stout, minutely cinereous to glabrate. Mature leaves divided nearly to the center, scabridulous and irregularly pellucid-maculate above, paler and inconspicuously hirtellous beneath, the lobes 9–11, conspicuously contracted toward the base, broadly obtuse to rounded at the tip, the petioles rather stout, densely and minutely puberulent, with the basal pulvinus densely ferruginous-velutinous. Staminate spadices in clusters of 12–15, up to about 10 cm. long and 4 mm. thick, with slender minutely puberulent-papillate stipes about 5–10 mm. long, the spathes oblongoid, shortly apiculate, about 12–14 cm. long shortly before anthesis, minutely subarachnoid-puberulent, the common peduncle about 5–7 cm. long shortly before anthesis, minutely pilosulose. Pistillate spadices about 10 cm. long in mature fruit (our specimen fragmentary), the common peduncle about 6–7 cm. long.

Known only from the type locality, in highland secondary forest.

CHIRIQUÍ: Boquete, *Maxon 5132, Davidson 862*.

The maculation of the leaves is most peculiar and possibly is pathological, but I have seen nothing comparable to it in other specimens of *Cecropia*. It may be similar to the cystolith maculations of Urticaceae.

5. CECROPIA OBTUSIFOLIA Bertol. Fl. Guat. 39. 1840.

Cecropia schiedeana Kl. in Linnaea 20:531. 1847.
Cecropia bicolor Kl. loc. cit. 1847.
Cecropia digitata Ten. ex Miq. in Mart. Fl. Bras. 4^1:149. 1853.
Cecropia commutata Schott, ex Miq. loc. cit. 148. 1853.
Cecropia mexicana Hemsl. Biol. Centr.-Am. Bot. 3:151. 1883.
Cecropia panamensis Hemsl. loc. cit. 1883.
Cecropia vogeleri Burret, in Notizbl. 9:49. 1924.
Cecropia mexicana var. *macrostachya* Donn. Sm. in Bot. Gaz. 27:442. 1899.

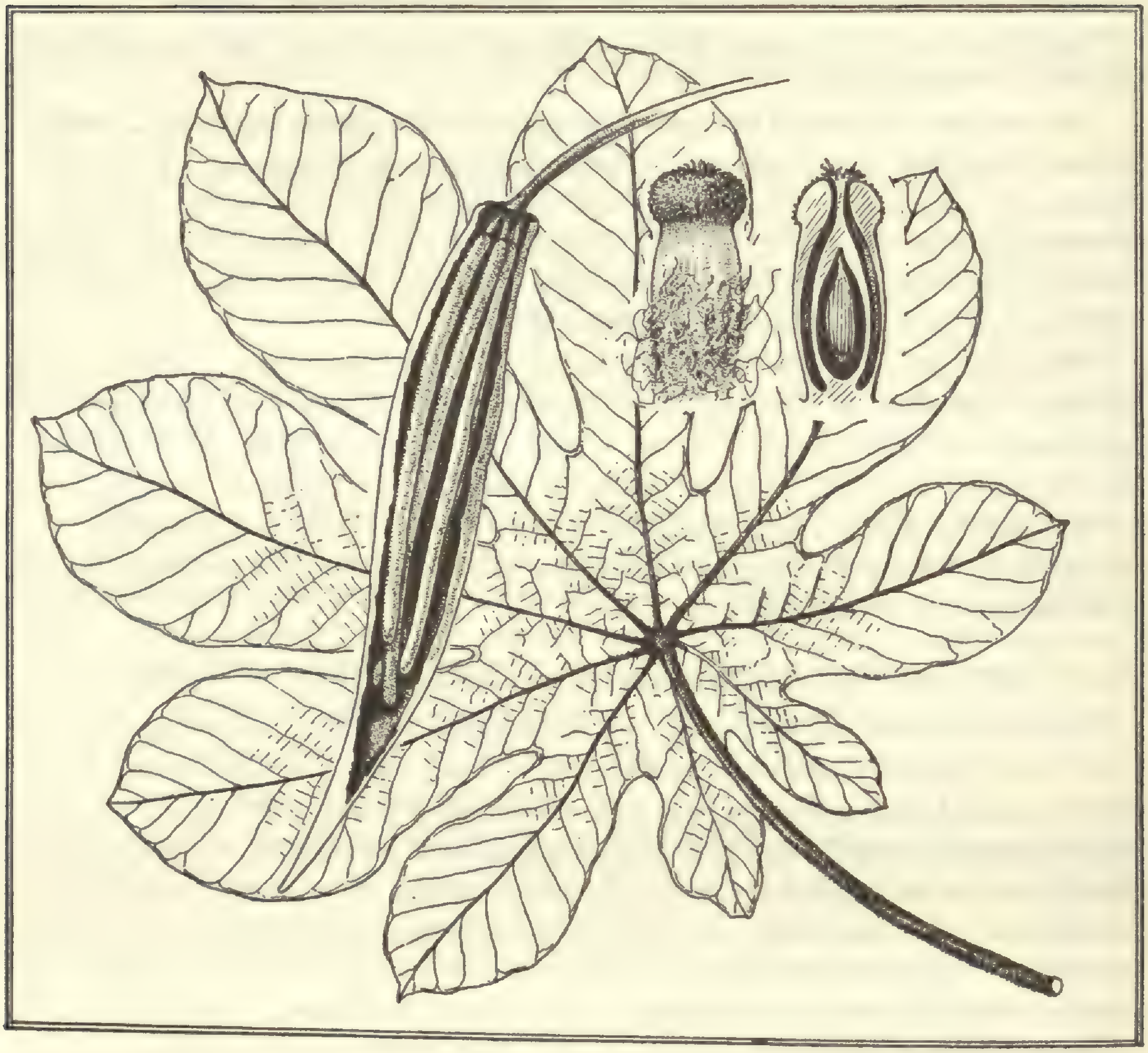

Fig. 61. *Cecropia obtusifolia*

Trees to about 10 m. tall or more, with stout seldom-branching trunks, the young branches stout, ferruginous-hirtellous to glabrate. Mature leaves divided nearly to the center, scabridulous above, paler and minutely cinereous beneath, the lobes usually 9–13, conspicuously contracted toward the base, rounded to shortly acuminate at the tip, the petioles rather slender, minutely ferruginous-hirtellous, with the basal pulvinus densely ferruginous-velutinous. Staminate spadices usually in clusters of 3, 12–16 cm. long and about 4 mm. thick, subsessile or with slender puberulent stipes to about 5 mm. long, the spathes 12–20 cm. long shortly before anthesis, narrowly oblongoid-fusiform and frequently somewhat falcate, rather sparsely arachnoid-villosulose, the common peduncle about 5–10 cm. long, relatively slender. Pistillate spadices in clusters of 3–4, 25–30 cm. long and about 5 mm. thick at anthesis, somewhat accrescent in fruit, sessile or with a very indefinite stipe, the spathes about 16–20 cm. long shortly before anthesis,

narrowly oblongoid-fusiform and frequently somewhat falcate, sparsely arachnoid-villosulose to glabrate, the common peduncle 8–14 cm. long, nearly glabrous.

Southern Mexico to northern South America, in lowland clearings, thickets and secondary forests.

BOCAS DEL TORO: Water Valley, *Von Wedel 771, 1559*. CANAL ZONE: Las Cruces Trail, *Hunter & Allen 462*; Gatún, *Standley 27304*; Masambí, *Pittier 2673*; Darién Station, *Macbride 2697*; Summit, *Harvey 5282*; Monte Lirio, *Christopherson 195*; Tabernilla, *Pittier 3826*; Barro Colorado Island, *Wetmore & Abbe 128, 204, Woodworth & Vestal 644, Kenoyer 309*. DARIÉN: Pinogana, *Allen 4311*. VERAGUAS: Santa Fé to Río Santa María, *Allen 4422*.

16. DORSTENIA L.

DORSTENIA L. Spec. Pl. 121. 1753.

Kosaria Forsk. Fl. Egypt.-Arab. 164. 1775.
Sychinium Desv. in Mem. Soc. Linn. Paris 4:216. 1826.

Succulent or subsucculent herbs. Leaves spiral, entire or variously lobed; stipules lateral. Flowers minute, monoecious, interspersed and immersed in a common discoid or radiate head, the obsolete perianths more or less concrescent with the receptacle. Staminate flowers with 1–3 minute stamens, the filaments inflexed before anthesis. Pistillate flowers with the ovary included and the excentric stigma shortly 2-lobed. Receptacles accrescent and fleshy in fruit, at length extruding the minute achenes.

Perhaps 75 or more very diverse species of the tropics of both hemispheres. In Panama only one species is presently known.

DORSTENIA CONTRAJERVA L. Sp. Pl. 121. 1753.

Dorstenia houstoni L. loc. cit. ed. 2. 176. 1762.
Dorstenia contrajerva var. *houstoni* (L.) E. Bur. in DC. Prodr. 17:259. 1873.
Dorstenia contrajerva ssp. *tenuiloba* S. F. Blake, in Contr. U. S. Nat. Herb. 24:2. 1922.
Dorstenia contrajerva var. *tenuiloba* (S. F. Blake) Standl. & Steyerm. in Field Mus. Bot. 23:40. 1944.

Succulent or subsucculent acaulescent or subacaulescent herbs. Leaves densely crowded, long-petioled, of relatively small or moderate size, extremely variable in dimensions and outline, commonly deeply pinnatifid, basifixed, usually scabridulous or inconspicuously puberulent. Receptacles on rather long slender peduncles, centrally peltate, variously radiate to nearly quadrangular, accrescent in fruit to as much as 5 cm. in diameter.

Southern Mexico to northern South America and in the Antilles, in moist thickets and forests from sea level to about 2,000 m. Widely known as *contrayerba* in Central America, which is a reflection of its use as a febrifuge.

BOCAS DEL TORO: Water Valley, *Von Wedel 1530*. CANAL ZONE: Las Cruces, *Seibert 574*; Ancón, *Pittier 2748*. COCLÉ: Cerro Valle Chiquito, *Seibert 502*. DARIÉN: Cana, *Williams 938*. PANAMÁ: Isla Taboga, *Woodson, Allen & Seibert 1505*; Juan Díaz, *Maxon & Harvey 6716*.

Far more frequent than the rather few citations imply.

Fig. 62. *Dorstenia contrajerva*

URTICACEAE

By ELLSWORTH P. KILLIP

Monoecious or dioecious herbs, shrubs, or trees, sometimes armed with stinging hairs and spines, usually bearing cystoliths; leaves simple, alternate or opposite (those of adjacent nodes or of a pair often unequal and dissimilar), entire, toothed, or rarely lobed, stipulate; flowers unisexual, small, greenish or greenish white, in unisexual or androgynous clusters, the perianth 2–5-lobed or parted or sometimes wanting; stamens as many as the perianth lobes and opposite them; ovary superior, 1-celled; style undivided, the stigma penicillate-capitate or filiform; fruit an achene, sometimes enclosed in the persistent perianth.

About 40 genera of the tropics and temperate zones of both hemispheres, including the stinging nettles, *picas* and *ortigas.* Here also may be included the Asian hemp and hashish plant, *Cannabis sativa* L., known as *marijuana* in Latin America, an erect herb with watery sap and digitately 5- to 9-divided leaves and inconspicuous dioecious flowers. Despite some attempts of the authorities, *marijuana* is grown more or less openly and used as a constituent of narcotic cigarettes.

a. Leaves opposite, those of a pair often unequal.
  b. Stigma short-penicillate; inflorescence paniculate, cymose, or capituliform .... 1. PILEA
  bb. Stigma filiform; flowers in sessile clusters in the leaf axils or in spikes. 2. BOEHMERIA
aa. Leaves alternate.
  b. Pistillate flowers with a perianth.
    c. Stigma sessile; plants usually armed with stinging hairs.
      d. Annual herbs; stigma becoming hooked in fruit.......... 3. FLEURYA
      dd. Trees, shrubs, or suffrutescent herbs; stigma penicillate.......... 4. URERA
    cc. Stigma filiform; plants without stinging hairs.
      d. Pistillate perianth nerveless; leaves toothed, those of the adjacent nodes often very unequal.......... 2. BOEHMERIA
      dd. Pistillate perianth strongly nerved; leaves entire (in Panama species), those of the adjacent nodes subequal.......... 5. POUZOLZIA
  bb. Pistillate flowers without a perianth.
    c. Flowers in axillary glomerules.......... 6. PHENAX
    cc. Flowers in long, slender spikes.......... 7. MYRIOCARPA

1. PILEA Lindl.

PILEA Lindl. Coll. Bot. *pl. 4.* 1821, nom. conserv.

Adicea Raf. Anal. Nat. 179. 1815, nom. rejic.

Annual or perennial, monoecious or dioecious herbs, sometimes suffrutescent, often succulent, without stinging hairs; stipules intra-axillary, deciduous or persistent; leaves opposite, usually petiolate, toothed or entire, those of a pair equal or markedly unequal, similar in shape or very dissimilar; flowers in unisexual or androgynous clusters, these solitary or forming cymes or panicles; staminate flowers 4 (rarely 2 or 3)-parted, the pistillate normally 3-parted, the middle segment usually larger than the lateral ones; stigma sessile, penicillate; achenes compressed, orbicular or ovate.

a. Leaves entire.
 b. Leaves orbicular to obovate, not more than 1 cm. long, 1-nerved or nerveless, succulent........ 1. P. MICROPHYLLA
 bb. Leaves ovate-lanceolate or elliptic, more than 1 cm. long, 3-nerved, membranous........ 2. P. PARIETARIA
aa. Leaves (at least the larger of a pair) toothed.
 b. Leaves of a pair dissimilar or very unequal, the larger more than twice as long as the smaller.
  c. Inflorescence sessile or subsessile, few-flowered; smaller leaves subentire........ 3. P. IMPARIFOLIA
  cc. Inflorescence peduncled, often branched; smaller leaves toothed.
   d. Leaves all distinctly petiolate; stipules persistent.
    e. Smaller leaves broadly ovate or suborbicular; stem drying straw-colored; plant glabrous throughout........ 4. P. CORNMANAE
    ee. Smaller leaves oblong; stem drying dark; plant usually pubescent toward tip of stem and on under side of leaf nerves........ 5. P. TRIANAEANA
   dd. Smaller leaves of a pair sessile or sub-sessile; stipules soon deciduous.
    e. Larger leaves oblanceolate, up to 2 cm. wide, their petioles not more than 5 mm. long; segments of staminate flowers with filiform tips........ 6. P. CHIRIQUINA
    ee. Larger leaves ovate or elliptic, 4–7 cm. wide, their petioles more than 5 mm. long; segments of staminate flowers not filiform-tipped........ 7. P. DONNELL-SMITHIANA
 bb. Leaves of a pair similar and equal, or if unequal the larger not more than twice as long as the smaller.
  c. Achenes 1–2 mm. long, strongly flattened.
   d. Leaves sessile or with a petiole much less than a third the length of the blade, often long-tapering at base........ 8. P. PTERICLADA
   dd. Leaves distinctly petiolate, rounded or abruptly narrowed at base.
    e. Stipules not more than 1.5 mm. long, soon deciduous; plants glabrous throughout; tips of staminate perianth segments minute........ 9. P. GRACILIPES
    ee. Stipules well developed and persistent or subpersistent; plants, especially the leaves, usually pubescent; staminate segments with long, filiform tips.
     f. Stem densely pubescent; leaves ovate or ovate-lanceolate, generally more than 2 cm. long, rugose........ 10. P. RUGOSISSIMA
     ff. Stem glabrous; leaves rhombic-ovate, generally not more than 2 cm. long, flat........ 11. P. AURICULATA
  cc. Achenes minute, scarcely more than 0.5 mm. long, only slightly flattened.
   d. Stem repent or trailing, with nearly equal internodes; leaves all orbicular........ 12. P. NUMMULARIFOLIA
   dd. Stem erect, repent only at base; at least the principal leaves ovate, obovate, rhombic, or elliptic.
    e. Inflorescence shorter than the petioles; plants essentially glabrous.
     f. Annual; leaves rhombic-ovate or ovate, thin, up to 4 cm. long; achenes stramineous, smooth........ 13. P. HYALINA
     ff. Perennial; leaves elliptic-lanceolate, thick, 8–20 cm. long; achenes black, papillose........ 14. P. PALLIDA
    ee. Inflorescence longer than the petioles; plants more or less pubescent.
     f. Leaves obovate, rounded at apex, the cystoliths on upper surface much more numerous toward the margin........ 15. P. INVOLUCRATA
     ff. Leaves ovate, ovate-lanceolate, or elliptic-lanceolate, acute or acuminate, rarely subobtuse, the cystoliths more evenly covering the upper surface.
      g. Leaves ovate-lanceolate or elliptic-lanceolate, averaging more than 4 cm. long, sharply dentate; plants usually dioecious........ 16. P. ACUMINATA
      gg. Leaves broadly ovate, averaging less than 4 cm. long, coarsely crenate-serrate; plants usually monoecious........ 17. P. PUBESCENS

1. Pilea microphylla (L.) Liebm. in Dansk. Vid. Selsk. Skrift. V. 2:296. 1851.

Parietaria microphylla L. Syst. ed. 10. 1308. 1759.
Pilea muscosa Lindl. Coll. Bot. *pl. 4*. 1821.

Glabrous, succulent, much-branched herb, up to 30 cm. high, variable in size and habit; leaves usually crowded throughout the length of the branches, entire, succulent, those of a pair unequal, the larger prevailingly obovate, up to 1 cm. long, petiolate, obtuse or subacute, tapering at base, the smaller orbicular or obovate-orbicular, rarely more than 3 mm. long, sessile or short-petioled; cystoliths linear, transverse across the leaf-blade; plants monoecious, rarely dioecious, the flower clusters very small, sessile or nearly so; achenes ovate, about 0.3 mm. long.

Throughout the American tropics, up to 2500 m. altitude, occurring in a variety of habitats, as in crevices of stone walls or pavements, on mossy roots or rocks, or on the forest floor; often cultivated as a border plant or in pots.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 358, 387*; Chiriquí Lagoon, *von Wedel 2487*. CANAL ZONE: Balboa, *Standley 28554, 29384* (cultivated; distributed as *P. serpyllacea*); Ancón, *Piper 6017*; Fort Sherman, *Standley 30946*; Barro Colorado Island, *Killip 40003*; *Shattuck 196* (cited as *P. serpyllacea*); Chagres, *Fendler 259*. COLÓN: Porto Bello, *Pittier 2447*. PANAMÁ: near Panamá, *Standley 26888, 29807, Heriberto 67*; between Las Sabanas and Matías Hernández, *Standley 31834*; Chepo, *Pittier 4460*.

A related species, *P. herniarioides* (Sw.) Lindl., may occur in Panama. It is distinguished by rhombic-orbicular leaves, the upper two or three pairs rosulate at the tip of the branches, the flower-clusters sessile within these rosettes. *Pilea serpyllacea* (H.B.K.) Liebm., also a related species, has been reported from Panama, but the records were apparently based on robust *P. microphylla*.

2. Pilea parietaria (L.) Blume, Mus. Bot. Lugd. 2:48. 1856.

Urtica parietaria L. Sp. Pl. 985. 1753.
Urtica ciliaris L. Sp. Pl. ed. 10, 1266. 1759.
Pilea ciliaris Wedd. in Ann. Sci. Nat. III. 18:209. 1852.

Plant herbaceous or suffrutescent; leaves of a pair (especially the petioles) somewhat unequal, the blades thin, elliptic or ovate-lanceolate, 2–8 cm. long, 1–3 cm. wide, rarely longer, acuminate at apex, rounded or subacute, sometimes subauriculate at base, 3-nerved, entire, usually ciliate, glabrous or sparingly strigillose with pellucid hairs, usually punctate beneath, the cystoliths linear or fusiform, usually inconspicuous; plants monoecious, the panicles 1 or 2 to an axil, shorter than the leaves, pedunculate, androgynous, or the upper almost wholly staminate and the lower pistillate; achenes minute, barely 0.5 mm. long.

Guatemala to Panama, on shaded banks and in moist forests, at altitudes between 1000 and 2000 m.; also in the West Indes.

CHIRIQUÍ: Quebrada Velo, alt. 1800 m., *Woodson & Schery 242*; Chiquero, Boquete District, *Davidson 549*.

3. Pilea imparifolia Wedd. in Ann. Sci. Nat. III. Bot. 18:212. 1852.

Decumbent or subrepent herb with numerous erect branches, essentially gla-

brous throughout; leaves of a node unequal and dissimilar, the larger rhombic-ovate to elliptic-oblong or obovate, 1–6 cm. long, 0.8–2 cm. wide, narrowed at apex, acute or attenuate at base, sessile or short-petioled, crenate-serrate above middle, the smaller leaves obovate-orbicular or orbicular-reniform, 0.6–1.5 cm. long, strongly asymmetrical, subentire; cystoliths linear on upper leaf surface, unequally punctiform beneath; plants dioecious, the cymes sessile or subsessile, few-flowered; achenes about 1 mm. long.

Panama to northern Peru, eastward to the Guianas and Amazonian Brazil; usually in dense forests.

COCLÉ: trail to Las Minas, north of El Valle de Antón, alt. 1000 m., climbing on trees and boulders, *Allen 2470*; El Valle de Antón, 1000 m., on tree trunk, *Alston 8791*.

This species is common in the forests of the Chocó, Colombia, where it shows much variation in shape and size of the leaves. Doubtless it occurs in Darién.

4. PILEA CORNMANAE Killip, in Jour. Washington Acad. Sci. 15:292. 1925.

Plant erect, up to 60 cm. high, glabrous throughout except the leaves, the stem as well as the foliage densely covered with elevated linear cystoliths; stipules orbicular or ovate, persistent; leaves coarsely serrate, dark green above, paler beneath, thin, sometimes sparingly strigillose above with hyaline hairs, the leaves of a node unequal and somewhat dissimilar, the larger ovate-lanceolate, 2–7 cm. long, 1.5–3 cm. wide, acuminate at apex, acute and often oblique at base, the petioles up to 4 cm. long, the smaller leaves broadly ovate or suborbicular, 1.5–2 cm. long, 1–1.5 cm. wide, acute; plants monoecious or dioecious, the flower-clusters unisexual, pedunculate; staminate heads globose, about 1 cm. wide, the segments long-caudate; pistillate flowers loosely clustered in subglobose heads; achenes broadly ovate or suborbicular, about 1 mm. long.

In wet forests of western Panama and San José Province, Costa Rica, between 1300 and 2000 m. alt.

CHIRIQUÍ: Holcomb's Trail, along Río Caldera, *Killip & Cornman* (*Killip 3543*, type); Cerro Horqueta, *von Hagen & von Hagen 2010*.

5. PILEA TRIANAEANA Wedd. in DC. Prodr. 16^1:121. 1869.

Stem repent below, at length erect, up to 20 cm. high, glabrescent or sometimes puberulent or strigillose above; leaves of a node similar in shape but at least the upper very unequal, oblong or oblong-lanceolate, acute or acuminate, usually acute at base, petiolate, crenate-serrate, glabrous, or sometimes pilose on the nerves beneath, the larger leaves 7–15 cm. long, 2–6 cm. wide, the smaller ones 1.5–4 cm. long, 0.5–1.3 cm. wide; plants dioecious; staminate flowers in dense globose heads which are solitary or form a branched cyme, the tips of the segments about 1.5 mm. long; pistillate flowers in lax, pedunculate panicles, the achenes 1–1.5 mm. long.

Panama and adjacent parts of Colombia, up to 1000 m. alt.

COCLÉ: vicinity of La Mesa, north of El Valle de Antón, 1000 m. alt., *Allen 2395*; El Valle de Antón, 1000 m. alt., *Alston 8786*.

6. Pilea chiriquina Killip, in Jour. Washington Acad. Sci. 15:291. 1925.

Fleshy herb, up to 1 m. high, slightly suffrutescent toward base, glabrous throughout; leaves dark green above, paler, sparingly punctate beneath, crenate-serrate, triplinerved, those of a pair unequal and dissimilar, the larger oblanceolate, 3–9 cm. long, 1–2 cm. wide, caudate-acuminate, subauricular at base, suboblique, the petioles up to 5 mm. long, the smaller leaves ovate or ovate-lanceolate, 0.7–3 cm. long, 0.5–1.5 cm. wide, acute, obliquely subcordate, sessile or subsessile; cystoliths minute, linear; plants dioecious, the flowers in compact peduncled cymes, the staminate perianth segments with filiform tips, the pistillate cymes smaller, the achenes broadly ovate, about 1 mm. long.

Panama; in wet highland forests, between 1400 and 2100 m. alt.

BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, *Allen 4914, 4915* (only ♂ collection known). CHIRIQUÍ: upper Río Caldera, *Killip 3546* (type); Bajo Chorro, *Woodson & Schery 668*; slopes of Cerro Horqueta, *Allen 4825*.

7. Pilea donnell-smithiana Killip, in Jour. Washington Acad. Sci. 15:292. 1925.

Erect herb, about 1 m. high, glabrous throughout; leaves ovate or elliptic, crenate-serrate nearly to base, rounded or subauriculate and often oblique at base, those of a node very unequal, the larger 10–20 cm. long, 4–7 cm. wide, caudate-acuminate, the petioles up to 2.5 cm. long, the smaller leaves up to 3 cm. long and 1.5 cm. wide, their petioles up to 5 mm. long; plants dioecious, the staminate flowers in small clusters in a small, few-branched panicle, the pistillate in few-flowered, short-peduncled, subglobose heads; achenes about 2 mm. long.

Costa Rica and adjacent parts of Panama; in wet forests at 1300 to 1700 m. alt.

CHIRIQUÍ: Holcomb's Trail, about 10 miles above El Boquete, *Killip 3562*.

A related species, *P. costaricensis* Donn. Sm., may occur in western Panama, material from Bajo Chorro, Chiriquí (*Davidson 56 and 717*), with very young inflorescence, perhaps being referable to it.

8. Pilea ptericlada Donn. Sm. in Bot. Gaz. 31:121. 1901.

Usually a stout herb, somewhat suffrutescent below, erect, up to 30 cm. high, glabrous throughout or fuscous-pubescent on the petioles and leaf-nerves; stipules orbicular-ovate, persistent; leaves of a node similar and subequal, oblong-elliptic or somewhat oblanceolate, 5–20 cm. long, 3–7 cm. wide, acuminate, cuneate-attenuate at base and sometimes long-decurrent on the petiole, coarsely crenate-serrate above middle, triplinerved, the petioles up to 1 cm. long; cystoliths mostly punctiform; plants dioecious, the inflorescence cymose-paniculate, borne in the upper axils, shorter than the leaves; staminate flowers long-pediceled, whitish, the lobes short-mucronate; pistillate flowers sessile, the achenes ovate, 1.5–2 mm. long, suboblique.

Costa Rica and Panama.

BOCAS DEL TORO: Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel 2203, 2237, 2318.* DARIÉN: Cana, alt. 750 m., *R. S. Williams 810.* CANAL ZONE: between Peluca Hydrographic Station and Quebrada Peluca, along Río Boquerón, *Steyermark & Allen 17252* (plant smaller in every way).

9. PILEA GRACILIPES Killip, in Jour. Washington Acad. Sci. 15:294. 1925.

Plants glabrous throughout; stem repent at base, the branches erect, up to 40 cm. high; leaves of a node similar in shape and subequal (or the smaller about three-quarters as long as the larger), lanceolate or ovate-lanceolate, 1–8 cm. long, up to 3 cm. wide, acuminate at apex, acute or somewhat rounded at base, crenate-serrate, the cystoliths linear, faint; plants monoecious or dioecious, the staminate and pistillate inflorescences often borne in the same axil, their peduncles very slender; staminate flowers in globose heads, 5–7 mm. wide, the pistillate in loose glomerules forming an interrupted spike, or racemose-paniculate; achenes lance-ovate, 1–1.5 mm. long.

Guatemala to Panama; in wet mountain-forests, 1500 to 4000 m. alt.

CHIRIQUÍ: Cerro Horqueta, 1700–2100 m., *Pittier 3230, 5426* (type); Volcán de Chiriquí, *Woodson, Allen & Seibert 894, Woodson & Schery 449, Davidson 1027*; Monte Lirio, *Seibert 293*; Bajo Chorro, *Woodson & Schery 659*; Quebrada Velo, *Woodson & Schery 243, 269*; between Casita Alta and Cerro Copete, *Woodson & Schery 347.*

10. PILEA RUGOSISSIMA Killip, in Proc. Biol. Soc. Washington 52:28. 1939.

Stem 30–100 cm. high, densely appressed-strigose; stipules oblong, persistent; leaves ovate or ovate-lanceolate, 1.5–6 cm. long, 1.5–3 cm. wide, acuminate at apex, rounded or cordulate at base, sharply serrate, strongly rugose, appressed-strigose between the veins of the upper surface, appressed-setose on the nerves and veins of the lower surface; plants dioecious, the staminate flowers sessile in a dense globose, peduncled head, the perianth about 5 mm. long, including prominent subulate tips.

Panama.

CHIRIQUÍ: Bajo Chorro, Boquete District, about 1800 m. alt., *Davidson 335* (type).

11. PILEA AURICULATA Liebm. in Dansk. Vid. Selsk. Skrift. V. 2:299. 1851.

Stem repent at base, with many slender, erect or decumbent branches; stipules ovate, persistent; leaves rotund-rhombic, 8–20 (rarely to 50) mm. long and wide, cuneate at base, coarsely crenate, strigillose with a few hyaline hairs above, the leaves of a node similar and subequal but one usually with a shorter petiole; plants usually dioecious, the flowers in small clusters up to 1 cm. wide, their peduncles generally exceeding the adjacent petioles; staminate flowers nearly 4 mm. long, including appendages about 1.2 mm. long; pistillate flowers with 1 of the segments larger than the others, auriculate; achenes broadly ovate, nearly 2 mm. long.

Southern Mexico, Guatemala, Costa Rica (where common), and western Panama; wet forests from 1500 to 3000 m. alt.

CHIRIQUÍ: Chiriquí Volcano, *Woodson, Allen & Seibert 934, Woodson & Schery 346, P. White 228*; Bajo Chorro, *Davidson 214.*

12. Pilea nummularifolia (Sw.) Wedd. in Ann. Sci. Nat. III. 18:255. 1852.

Urtica nummularifolia Sw. in Svensk. Vet. Akad. 8:63, *pl. 1, f. 2.* 1787.

Stem repent or trailing, rooting at most of the nodes, villosulous; stipules persistent; leaves almost orbicular, 5–12 mm. wide, crenate, usually strigillose with stiff, hyaline hairs on both surfaces, the cystoliths inconspicuous; plants dioecious or occasionally monoecious, the staminate flowers usually clustered in the uppermost axils, the pistillate in dense, short-peduncled cymes; achenes barely 0.4 mm. long.

West Indies to Venezuela and Amazonian Peru; sometimes cultivated.

canal zone: in Powell's garden, *Standley 28555, 41191.*

13. Pilea hyalina Fenzl, in Denkschr. Akad. Wiss. Math. Naturw. (Wien) 1: 256. 1850.

Slender, erect annual, 10–30 cm. high, the stem simple, glabrous; stipules very small, soon deciduous; leaves rhombic-elliptic or ovate, 1–4 cm. long, 0.8–2.5 cm. wide (extremes up to 6 × 4 cm.), acute at apex, cuneate at base, serrate except toward the base, thin-membranous, glabrous, or sparsely hyaline-strigose above; plants monoecious, the inflorescences androgynous, cymose-paniculate, shorter than the petioles, borne at nearly every node, the staminate flowers relatively few; achenes suborbicular, not more than 0.5 mm. long.

Fig. 63. *Pilea auriculata*

Widely distributed in the American tropics, from Mexico and the Lesser Antilles to Chile, Argentina, and Brazil, up to 1500 m. alt.

BOCAS DEL TORO: Changuinola Valley, in garden, *Dunlap 399*. CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 25764*.

This species has been confused with *P. pumila* Gray, of the United States; the plant from Santiago de Veraguas, cited as *P. pumila* by Seeman (Bot. Voy. Herald 194), is undoubtedly *P. hyalina*.

14. PILEA PALLIDA Killip, in Jour. Washington Acad. Sci. 15:295. 1925.

Plant erect, 30 cm. or more high, essentially glabrous throughout; leaves elliptic-lanceolate, 8–20 cm. long, 3–7 cm. wide, caudate-acuminate, acute at base, sometimes suboblique, serrate, densely covered with fusiform and punctiform cystoliths, slightly silvery-lustrous and punctate beneath, the petioles up to 7 cm. long; plants dioecious; staminate flowers densely congested in globose, sessile clusters, the perianth 1.5–2 mm. long including tips about half as long; pistillate flowers in much-branched cymes, shorter than the petioles, the achenes about 0.6 mm. long, black, minutely papillose.

Panama and Costa Rica; in forests, 1000–1400 m. alt.

BOCAS DEL TORO: Sibubi Falls, Sixaola Valley, *Rowlee & Rowlee 376* (type). COCLÉ: El Valle de Antón, 1000 m. alt., *Alston 8797*.

15. PILEA INVOLUCRATA (Sims) Urban, Symb. Antill. 1:298. 1899.

Urtica involucrata Sims, Bot. Mag. 51: *pl. 2481*. 1824.
Pilea chrysosplenioides Wedd. in Ann. Sci. Nat. III. 18:231. 1852.
Pilea pubescens var. *involucrata* Wedd. in DC. Prodr. 16^1:153. 1869.

Stem repent at base, the branches ascending, up to 30 cm. high, appressed-hirsute above; leaves massed at end of branches, obovate or rotund-ovate, up to 5 cm. long and 3.5 cm. wide, rounded at apex, rounded or subauriculate at base, short-petioled, finely crenate, ciliate, strigillose with appressed hyaline hairs (rarely glabrate) above, sparingly to densely pubescent beneath, especially on the nerves, the cystoliths on the upper surface linear or fusiform and confined to the margin; plants monoecious or dioecious, the cymes generally unisexual, sessile or subsessile, shorter than the leaves; achenes minute, less than 0.5 mm. long.

Panama and the West Indies to Colombia and Venezuela, usually below 1000 m. alt.; cultivated in the United States.

CANAL ZONE: Empire, *Crawford 574*; Salamanca Hydrographic Station, Río Pequení, *Woodson, Allen & Seibert 1600*.

16. PILEA ACUMINATA Liebm. in Dansk. Vid. Selsk. Skrift. V. 2:302. 1851.

Stem subrepent at base, the branches erect, 20–40 cm. high, glabrous, or sparingly pubescent in upper part; leaves ovate-lanceolate, 4–10 cm. long, 2–3 cm. wide (extremes to 15 × 6 cm.), acuminate, cordate or somewhat narrowed at base, coarsely serrate, sometimes bullate, usually strigillose with a few hyaline hairs above, hirsutulose on the nerves beneath; plants usually dioecious, the cymes

diffusely branched, with peduncles up to 6 cm. long; staminate flowers with filiform appendages; achenes minute, barely 0.5 mm. long.

Mexico to Colombia; in wet shady places, between 600 and 1000 m. alt.

COCLÉ: El Valle de Antón, *Allen 1737, Alston 8792.*

17. PILEA PUBESCENS Liebm. in Dansk. Vid. Selsk. Skrift. V. 2:302. 1851.

Stem repent, at length erect and usually with several erect or ascending branches, brownish-pubescent; leaves usually massed at the end of the stem or branches, wanting or much reduced below, broadly ovate, up to 7 cm. long and 6 cm. wide, petiolate, usually coarsely crenate-serrate, often ciliate, sparingly strigillose with hyaline hairs or rarely glabrous above, hirsutulous beneath on the nerves and veins, the cystoliths linear and fusiform above, obscure beneath; plants monoecious or occasionally dioecious, the flowers in dense globose clusters forming a panicle up to 7 cm. long, slender-peduncled, the panicles usually androgynous with relatively few staminate flowers, the achenes minute, scarcely 0.5 mm. long.

Pilea pubescens evidently has a wide distribution in the lowland tropics although doubtless much material has been wrongly referred to it. Direct comparison has been made between the Panama specimens here cited and the type, collected in southeastern Brazil by Lund and generously lent the author by the Botaniske Museum, Copenhagen, and there is perfect agreement.

CHIRIQUÍ: El Boquete, 1200 m. alt., *Davidson 860.* COCLÉ: El Valle de Antón, *Alston 8781.* DARIÉN: Cana, *R. S. Williams 837.*

2. BOEHMERIA Jacq.

BOEHMERIA Jacq. Enum. Pl. Carib. 9. 1760; Stirp. Amer. 246, *pl. 157.* 1763.

Trees, shrubs, or perennial herbs, unarmed and without stinging hairs; leaves opposite or alternate, toothed, 3-nerved, those of the adjacent nodes sometimes unequal and dissimilar; plants monoecious or dioecious, the flowers in globose, usually unisexual clusters in the axils of the leaves or forming a spike; staminate flowers 3 or 4 (rarely 5)-parted; pistillate flowers tubular, contracted at the throat, 2–4-toothed or entire, the stigma filiform, the achene enclosed in the persistent, sometimes enlarged perianth.

a. Flower-clusters forming a spike, often leafy at summit; leaves opposite on stem, alternate or branched; plants herbaceous........ 1. B. CYLINDRICA
aa. Flower-clusters axillary on the main stem and leafy branches; leaves alternate; shrubs, trees, or suffrutescent herbs.
 b. Leaves coriaceous, bullate........ 2. B. ASPERA
 bb. Leaves membranous or subcoriaceous, flat or slightly rugulose.
  c. Leaves of adjacent nodes very unequal and dissimilar, the smaller, ones orbicular or subreniform, sessile........ 3. B. ULMIFOLIA
  cc. Leaves of adjacent nodes similar or nearly so, though unequal, all petiolate or the smaller leaves sometimes subsessile in *B. pavonii.*
   d. Leaves membranous, coarsely serrate; staminate perianth 3-lobed........ 4. B. CUSPIDATA
   dd. Leaves subcoriaceous, finely serrulate or sub-entire; staminate perianth 4-lobed........ 5. B. PAVONII

1. Boehmeria cylindrica (L.) Sw. Prodr. 34. 1788.

Urtica cylindrica L. Sp. Pl. 984. 1753.

Erect herb up to 1.5 m. high, the stem simple or branched; leaves opposite on the stem, alternate on the branches, narrowly lanceolate, ovate-lanceolate, or ovate, up to 18 cm. long and 7 cm. wide, acuminate at apex, rounded, subcordate, or subtruncate at base, coarsely dentate or serrate-dentate, glabrous, or puberulent beneath on the nerves; flower-clusters sessile in an erect or ascending spike which often is leafy toward the tip; plants monoecious; staminate perianth 4-lobed; pistillate perianth rotund-obovate, 1.5–2 mm. long and broad, 4-toothed, compressed, nearly sessile.

Eastern Canada; eastern and southern United States; Mexico to Panama; West Indies; southeastern Brazil.

bocas del toro: Changuinola Valley, *Dunlap 365*. canal zone: Barro Colorado Island, *Standley 41177*, *Starry 255*.

2. Boehmeria aspera Wedd. in Arch. Mus. Paris 9:349. *p. 11, f. 24–28*. 1856.

Shrub or suffrutescent herb, 1–3 m. high; leaves alternate, those of the adjacent nodes very unequal and somewhat dissimilar, crenate-serrate, coriaceous, strongly bullate, smooth or hispid above, densely cano-hirsute beneath, the larger lanceolate, 4–15 cm. long, 1–4 cm. wide, long-acuminate, the smaller leaves ovate, 1–5 cm. long, 1–2.5 cm. wide, acute; plants monoecious, the flower-clusters predominantly pistillate; staminate perianth 4-lobed; pistillate perianth about 1 mm. long, sericeo-pubescent at throat, bidentate.

Costa Rica to Peru.

chiriquí: vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., *Woodson & Schery 560*.

3. Boehmeria ulmifolia Wedd. in Ann. Sci. Nat. IV. 1:202. 1854.

Boehmeria fallax var. *ulmifolia* Wedd. in DC. Prodr. 16^1:198. 1869.

Shrub or small tree up to 6 m. high, with slender, more or less pubescent branches; leaves serrate, thin, appressed-hispidulous above, pilosulous or puberulent beneath, those of adjacent nodes strongly dimorphic and unequal; larger leaves elliptic-ovate, 5–15 cm. long, 1.5–5 cm. wide, cuspidate-acuminate, acute or rounded at base, somewhat oblique, with slender petioles 5–20 mm. long, the smaller leaves (often soon deciduous) orbicular or subreniform, 5–10 mm. long and broad, usually emarginate at base, sessile; plants monoecious or dioecious, the flower-clusters axillary, generally unisexual; staminate perianth 4-lobed; pistillate perianth about 2 mm. long, stipitate, very slightly compressed, bidentate.

Southern Mexico to Panama, from about 1000 to 2000 m. alt., ascending higher in western Panama.

bocas del toro: Robalo Trail, northern slopes of Cerro Horqueta, alt. 1800–2100 m., *Allen 4913* (tentatively referred here). chiriquí: upper Chiriquí Viejo valley, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 183*; Potrero Muleto to summit, Volcán de Chiriquí, alt. 3500–4000 m., *Woodson & Schery 465*.

4. BOEHMERIA CUSPIDATA Wedd. in Arch. Mus. Paris 9:345. 1856.

Boehmeria ramiflora var. *cuspidata* Wedd. in DC. Prodr. 16^1:197. 1869.

Slender shrub or suffrutescent herb, up to 3 m. high, the stem appressed-pubescent; leaves of adjacent nodes similar but unequal, cuspidate-acuminate, coarsely serrate, entire toward the cuneate or slightly rounded, suboblique base, appressed-hispidulous above, sparingly pilosulous beneath, the larger leaves 6–15 cm. long, 2–5 cm. wide (smaller on the branches), the petioles slender, up to 5 cm. long, the smaller leaves 3–5 cm. long, 1.5–2.5 cm. wide, the petioles up to 1.5 cm. long; plant monoecious (or dioecious?), the flower-clusters axillary; staminate perianth 3-lobed; pistillate perianth elliptic, about 1.5 mm. long, narrowly margined, bidentate.

Southern Mexico to Panama.

PANAMÁ: hills above Campana, alt. 600–800 m., *Allen 1310*.

5. BOEHMERIA PAVONII Wedd. in Ann. Sci. Nat. IV. 1:202. 1854.

Shrub or small tree, 2–6 m. high, the branches finely appressed-pubescent;

Fig. 64. *Boehmeria ulmifolia*

leaves alternate (those of the adjacent nodes similar or nearly so though quite unequal), finely serrulate or sometimes subentire, subcoriaceous, finely appressed-hispidulous above, usually appressed sericeo-pubescent on the nerves and veins beneath and puberulent in the areoles, the larger leaves oblong-lanceolate or elliptic-lanceolate 4–16 cm. long, 1.5–4.5 cm. wide, attenuate-acuminate, the petioles 1–2.5 cm. long, the smaller leaves similar though sometimes ovate, subsessile, and merely acute; plants dioecious, rarely monoecious, the clusters generally unisexual; staminate perianth 4-lobed; pistillate perianth attenuate at base, narrowly margined.

Guatemala and Panama; Peru and Bolivia.

CHIRIQUÍ: El Boquete, alt. 1150 m., *Davidson 830.*

3. FLEURYA Gaud.

FLEURYA Gaud. Voy. Uran. Bot. 497. 1826.

Annual herbs, usually with stinging hairs; leaves alternate, petiolate, toothed, trinerved; plants monoecious or dioecious; flowers in androgynous or unisexual clusters in large panicles; staminate perianth 4–5-parted, with 4–5 stamens; pistillate perianth with 4 imbricated segments, the stigma papillose, at length hooked, the achenes oblique, compressed.

Fig. 65. *Fleurya aestuans*

1. Fleurya aestuans (L.) Gaud. Voy. Uran. Bot. 497. 1826.

Urtica aestuans L. Sp. Pl. ed. 2. 1397. 1762.

Plant generally terrestrial, erect, simple or few-branched, up to 2 m. high, with stinging hairs usually present, the stem sometimes glandular; leaves broadly ovate, rarely ovate-lanceolate, up to 18 cm. long and 12 cm. wide, acute or acuminate, usually rounded at base, coarsely and sharply dentate, thin-membranous, the petioles up to 12 cm. long; panicles often much longer than the petioles; achenes 1–1.5 mm. long.

Widely distributed in the tropics at low elevations; often occurring in waste places.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1269, 2848.* CANAL ZONE: San Pablo, *Pittier 4063*; Ancón, *Pittier 2751*; Balboa, *Standley 25286, 25601, 26981*; Gamboa, *Standley 28305.* CHIRIQUÍ: Puerto Armuelles, *Woodson & Schery 849.* DARIÉN: Boca de Cupe, *Allen 873.* PANAMÁ: Bella Vista, *Killip 39944*; Exposición, *Heriberto 279*; Corozal road, *Standley 26765*; Tumba Muerto road, *Standley 29707*; Las Sabanas, *Paul 32*; Chepo, *Pittier 4767.* VERAGUAS: Isla de Coiba, *Mendez 128.*

4. URERA Gaud.

Urera Gaud. Voy. Uran. Bot. 496. 1826.

Trees or shrubs, rarely scandent, usually with stinging hairs or stout prickles; stipules free, or more or less connate; leaves alternate, petiolate, 3- or 5-nerved at base, penninerved above, the cystoliths punctiform, linear, or wanting; plants usually dioecious, the flowers in axillary, dichotomous or irregularly branched cymes or panicles; staminate flowers with a 4–5-parted perianth and 4–5 stamens and a rudimentary ovary; pistillate flowers with 4 equal or unequal segments, the stigma penicillate-capitate, persistent; achenes straight or oblique, at least partially surrounded by the fleshy, enlarged perianth.

a. Leaves incised-lobed usually more than halfway to the midnerve............ 1. U. LACINIATA
aa. Leaves not lobed, dentate, crenate, or subentire.
b. Achenes more than 2 mm. long; leaves coarsely dentate or sinuate-dentate; plants usually with stout prickles or spines........................... 2. U. BACCIFERA
bb. Achenes less than 2 mm. long; leaves crenate, crenate-dentate, or subentire.
c. Leaves broadly ovate to orbicular-ovate, usually cordate; pistillate inflorescences usually long-peduncled and equaling the adjacent petioles, the flowers in glomerules.. 3. U. CARACASANA
cc. Leaves ovate-oblong to elliptic-ovate, rounded or slightly emarginate at base; pistillate inflorescences much shorter than the petioles, the flowers separate, pedicellate.. 4. U. ELATA

1. Urera laciniata (Goudot) Wedd. in Ann. Sci. Nat. III. 18:203. 1852.

Urtica laciniata Goudot, ex Wedd. loc. cit., as synonym.
Urera girardiniodes Seem. Bot. Voy. Herald 194. 1854.

Low tree, shrub, or erect herb, 1–4 m. high, the branches densely covered with stout bristles or spines; leaves 15–35 cm. long and wide, deeply incised-lobed (lobes acuminate, entire or few-toothed), spiny on the nerves beneath, membranous, glabrescent; inflorescence paniculate, up to 20 cm. long; staminate flowers in glomerules, the pistillate in glomerules or often distinct, sessile; achenes about 1.5 mm. long, suboblique.

Costa Rica to Venezuela and Peru, at low altitudes.

CANAL ZONE: Las Cruces, *Seemann 872* (type of *U. girardiniodes*).

2. URERA BACCIFERA (L.) Gaud. Voy. Uran. Bot. 497. 1826.

Urtica baccifera L. Sp. Pl. ed. 2. 1398. 1762.

Coarse, erect, subligneous herb, or a shrub or small tree, 1–6 m. high, the stem usually covered with short, stout prickles; leaves broadly ovate or round-ovate to oblong-ovate, up to 35 cm. long and 25 cm. wide, rounded or cordate at base, coarsely dentate or irregularly sinuate-dentate, usually with scattered stinging hairs above and with such hairs or prickles on the nerves beneath; plants dioecious, the flowers in much-branched cymes; fruit succulent, 3–5 mm. long, white or rose-colored.

Widely distributed in tropical America. The hairs are very painfully stinging.

CANAL ZONE: Ancón, *Piper 6000*; Fort Sherman, *Standley 31160*. COLÓN: Lagarto, *Cowell 257*. DARIÉN: Pinogana, *Allen 926*; Marraganti, *R. S. Williams 692*. PANAMÁ: Taboguillo Island, *Miller 2001*; sabanas near Panamá, *Paul 361*; Juan Díaz, *Standley 30536*; Río Tecumen, *Standley 26692, 26732*; Río Tapia, *Standley 28244*.

3. URERA CARACASANA (Jacq.) Griseb. Fl. Brit. W. Ind. 154. 1859.

Urtica caracasana Jacq. Hort. Schoenbr. 3:71. *pl. 396.* 1798.
Urtica verrucosa Liebm. in Vidensk. Selsk. Skr. V. 2:295. 1851.
Urera jacquini Wedd. in Ann. Sci. Nat. III. 18:200. 1852.

Shrub or small tree, 2–10 m. high, with elongate branches, the young twigs, petioles, inflorescence, and leaf nerves usually armed with stinging hairs; leaves broadly ovate to ovate-lanceolate, up to 30 cm. long and 25 cm. wide, acuminate, cordate or cordulate at the base (basal lobes sometimes overlapping), crenate-dentate, scabrous, sometimes verrucose, above, more or less pubescent beneath; plants dioecious, the cymes regularly dichotomous; staminate flowers sessile in distinct, compact glomerules; pistillate flowers sessile or pedicillate in compact glomerules (rachis and segments sometimes becoming enlarged), the segments usually densely covered with white, punctiform cystoliths; achenes 0.5–1 mm. long.

Widely distributed in continental tropical America from sea level to 2000 m. altitude. The species is here interpreted in a very broad sense, and the specimens cited show considerable variation in shape and texture of the leaves, presence or absence and nature of the foliar cystoliths, degree of pubescence, arrangement of the flowers, and size of the achenes. The American species of *Urera* are greatly in need of taxonomic revision.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 174*; Nievecita, *Woodson, Allen & Seibert 1849*; Darkland, *von Wedel 1*; Water Valley, *von Wedel 686*. CANAL ZONE: Mamei Hill, *Pittier 3804*. CHIRIQUÍ: Puerto Armuelles, *Woodson & Schery 863*; between Paso Ancho and Monte Lirio, upper Río Chiriquí Viejo valley, *Allen 1471* (variant described as *Urtica verrucosa* Liebm.); Cerro Galera Chorcha, near Gualaca, *Allen 5063*; Bajo Chorro Boquete District, *Davidson 349*. COLÓN: Río Fató, *Pittier 3899*. DARIÉN: Boca de Cupe, *Allen 911*, *R. S. Williams 716*; Cana, *R. S. Williams 815*; Yape, *Allen 855*; headwaters of Río Chico, *Allen 4592*. PANAMÁ: Juan Díaz, *Standley 30487*; Arenoso, lower Río Trinidad, *Seibert 608*.

4. URERA ELATA (Sw.) Griseb. Fl. Brit. W. Ind. 154. 1859.

Urtica elata Sw. Prodr. 37. 1788.

Shrub or small tree, 2–4 m. (occasionally to 6 m.) high, sometimes becoming scandent; leaves ovate-oblong to elliptic-ovate, up to 30 cm. long and 12 cm. wide, acuminate at apex, rounded at base, sometimes slightly emarginate, crenate-serrate, crenulate, or subentire, glabrescent, or occasionally hirsutulous on the principal nerves beneath; plants dioecious, the inflorescences dichotomous, much shorter than the petioles, staminate flowers sessile in glomerules, glabrous; pistillate flowers short-pediceled, usually borne singly.

With much the same distribution in Panama as the preceding species; also in Jamaica and Colombia.

Two forms are represented by the specimens cited below; one has relatively small leaves which bear punctiform cystoliths densely massed all over the upper surface, and agrees best with type material of *U. elata* in the British Museum; the other has leaves generally more than 15 cm. long, the cystoliths being short-linear and radiating from the center of the areoles to the veinlets. This latter variant has been confused with *U. alceifolia* (Poir.) Gaud., of French Guiana, which apparently cannot be separated from the common *U. caracasana.*

Fig. 66. *Urera elata*

BOCAS DEL TORO: Changuinola Valley, *Dunlap 241*; Río Cricamola, between Finca St. Louis and Konkintoë, alt. 10–50 m., *Woodson, Allen & Seibert 1923*. CANAL ZONE: *Hayes 750*; Barro Colorado Island, *Standley 41132, Kenoyer 396*; Madden Dam, *Allen 2008*. CHIRIQUÍ: vicinity of Bajo Mona, alt. 1500–2000 m., *Woodson & Schery 593, Woodson, Allen & Seibert 1005*; near Monte Lirio, Río Chiriquí Valley, *G. White 63*; Progreso, *Cooper & Slater 176*; El Boquete, alt. 1000–1300 m., *Maxon 4992, Pittier 2939*. COCLÉ: El Valle de Antón, trail to Las Minas, alt. 1000 m., *Allen 2461, 2712*; vicinity of Finca Tomás Arias, alt. 600 m., *Allen 3617*. COLÓN: Río Fató, alt. 10–100 m., *Pittier 4189*. DARIÉN: Cana, *R. S. Williams 794*.

5. POUZOLZIA Gaud.

POUZOLZIA Gaud. Voy. Uran. Bot. 503. 1826.

Leucococcus Liebm. in Dansk. Vid. Selsk. Skrift. V. 2:311. 1851.
Margarocarpus Wedd. in Ann. Sci. Nat. IV. 1:203. 1854.

Low shrubs, rarely woody vines; stipules free, often persistent; leaves alternate (in American species), entire or rarely toothed; petiolate, trinerved, densely covered with punctiform cystoliths above; plants usually monoecious, the flowers in small clusters, in the leaf axils or forming spikes; staminate perianth depressed-globose in bud, 3–5-parted or -lobed, the stamens 3–5; pistillate perianth tubular, contracted at the throat, 2–4 toothed, completely enclosing the ovary, strongly nerved, the stigma pubescent on one side, the achenes crustaceous, shiny.

a. Leaves white-tomentose beneath, long-petiolate.................................... 1. P. GUATEMALANA
aa. Leaves not white-tomentose.
  b. Petioles not more than 1 cm. long; base of leaves oblique and usually subemarginate.................................... 2. P. OBLIQUA
  bb. Petioles much more than 1 cm. long; base of leaves not oblique, cuneate or rounded.................................... 3. P. OCCIDENTALIS

1. POUZOLZIA GUATEMALANA (Blume) Wedd. in DC. Prodr. 16^1:233. 1869.

Boehmeria guatemalana Blume, Mus. Bot. Lugd. Bat. 2:206. 1856.

Slender shrub; branches hirsutulous; leaves lanceolate or ovate-lanceolate, 6–15 cm. long, 2–4.5 cm. wide, caudate-acuminate, obtuse or acute at base, entire, sometimes bullate, asperate above, pilose on the nerves and veins and white-tomentose elsewhere beneath; petioles 2–5 cm. long, very slender; glomerules androgynous; staminate flowers 4-merous, the pistillate 4-toothed.

Guatemala to Panama, lowlands of the Atlantic side; rare.

BOCAS DEL TORO: beyond Río San Juan, Changuinola Valley, *Dunlap 457*.

2. POUZOLZIA OBLIQUA (Poepp.) Wedd. in Arch. Mus. Paris 9:405. 1857.

Margarocarpus obliquus Poepp. et Wedd. Ann. Sci. Nat. IV. 1:204. 1854. (*Boehmeria obliqua Poepp.*, nom. nud. as synonym).

Shrub or small tree, 1–5 m. high, densely hirsute nearly throughout, the branches sometimes scandent; leaves oblong or oblong-lanceolate, 2–15 cm. long, 1–5 cm. wide, entire, attenuate-acuminate at apex, oblique and usually emarginate at base, scabrous above, the petioles up to 1 cm. long; flower clusters androgynous or unisexual; staminate flowers 4-merous; achenes light brown or white, the styles 7–10 mm. long.

Fig. 67. *Pouzolzia obliqua*

Guatemala to Venezuela and Peru, at low elevations; common in the Canal Zone; forests and thickets.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1434, 2597*; Changuinola Valley, *Dunlap 370*. CANAL ZONE: Barro Colorado Island, *Kenoyer 327, Aviles 24b*; Balboa, *Standley 25410, 25587, 29265*; Mamei Hill, *Pittier 3792*; Río Pedro Miguel, *Standley 29976*; Las Cascadas Plantation, *Standley 25783*; Cerro Gordo, near Culebra, *Standley 25972*; Gamboa, *Pittier 6651, Standley 28306*; Darién Station, *Standley 31606*; Las Cruces Trail, *Standley 29070*; Cocoli, *Riley 128*.

3. POUZOLZIA OCCIDENTALIS (Liebm.) Wedd. in Arch. Mus. Paris 9:410. 1857.

Leucococcus occidentalis Liebm. in Dansk. Vid. Selsk. Skrift. V. 2:311. 1851.

Shrub or small tree, up to 5 m. high, the branches densely hirsutulous to nearly glabrous; leaves elliptic-lanceolate to broadly lanceolate-ovate, 7–15 cm. long, 3–9 cm. wide, acuminate at apex, cuneate or rounded at base, entire, appressed-pubescent above with stiff scattered hairs, more or less pilosulous beneath, especially on the nerves and at the margin; petioles slender, 2–8 cm. long; glomerules androgynous, rarely unisexual, few-flowered, the staminate flowers 4-merous.

Honduras to Colombia and Venezuela; also in Puerto Rico. In forests and thickets at low elevations.

DARIÉN: Boca de Cupe, 40 m. alt., *Allen 868*. PANAMÁ: Taboga Island, *Pittier 3530, Standley 27923*.

6. PHENAX Wedd.

PHENAX Wedd. in Ann. Sci. Nat. IV. 1:191. 1854.

Unarmed shrubs or suffrutescent herbs; leaves alternate, petiolate, toothed, rarely entire, the cystoliths mainly punctiform; plants monoecious or dioecious, the flowers in dense, sessile, axillary clusters; staminate flowers usually 4-lobed; pistillate flowers without a perianth, the small achene sessile and subtended by a brown, scarious bractlet, the stigma elongate-filiform, persistent.

a. Plants dioecious; leaves narrowly lanceolate, minutely serrulate, attenuate-acuminate.......... 1. P. ANGUSTIFOLIUS
aa. Plants monoecious; leaves ovate or ovate-lanceolate, coarsely crenate-serrate or crenulate-serrate.
  b. Leaves ovate-lanceolate, narrowed at base, flat, glabrous except occasionally for a few hairs on the nerves beneath; stem glabrous.......... 2. P. MEXICANUS
  bb. Leaves ovate, rounded or cordulate at base, more or less rugose, densely pubescent beneath; stem hirsute.......... 3. P. RUGOSUS

1. PHENAX ANGUSTIFOLIUS (H.B.K.) Wedd. in Ann. Sci. Nat. IV. 1:193. 1854.
Boehmeria angustifolia H.B.K. Nov. Gen. & Sp. 2:34. 1817.

Shrub or suffrutescent herb, up to 3 m. high; leaves narrowly lanceolate, 5–15 cm. long, 0.5–5 cm. wide, attenuate-acuminate, minutely serrulate, entire toward base, thin membranous, glabrous above, very sparingly strigillose on the nerves and veins beneath, the petioles very slender; plants dioecious; achenes minute, about 0.3 mm. long, the styles 4–5 mm. long.

Costa Rica to Peru and Bolivia, usually at elevations of less than 800 meters.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 371*. COCLÉ: vicinity of El Valle, 100–800 m. alt., *Allen 764*.

2. PHENAX MEXICANUS Wedd. in Ann. Sci. Nat. IV. 1:193. 1854.

Shrub, 2–6 m. high, glabrous throughout except occasionally on the under side of the leaf nerves and veins; leaves ovate-lanceolate, up to 15 cm. long and 5 cm. wide, acuminate, narrowed at base, crenate-serrate except toward base, membranous or subcoriaceous, the petioles up to 5 cm. long, usually much shorter; plants monoecious; achenes about 0.8 mm. long.

Southern Mexico to western Panama, usually at elevations of more than 800 meters.

CHIRIQUÍ: El Boquete, *Maxon 4995, Pittier 2881, Davidson 452*; Finca Lérida to Peña Blanca, *Woodson & Schery 312*; valley of the upper Río Chiriquí Viejo, P. *White 340*.

A related species, P. *hirtus* (Sw.) Wedd., a common plant of the tropics, apparently has not yet been collected in Panama.

3. PHENAX RUGOSUS (Poir.) Wedd. in DC. Prodr. 16^1:235^{38}. 1869.
Procris rugosa Poir. in Lam. Encycl. 5:628. 1804.
Boehmeria rugosa Pers. Synops. 2:556. 1807.

Shrub, 1–3.5 m. high, the stem stout, densely hirsute; leaves ovate, 3–12 cm. long, 1–7 cm. wide, acute or acuminate at apex, rounded or rarely cordulate at base, crenate-serrate, rugose, usually villous-tomentose beneath; plants monoecious, the glomerules very dense; achenes about 0.5 mm. long.

Fig. 68. *Phenax rugosus*

Southern Mexico to Venezuela and Bolivia, usually occurring above 1000 m. altitude.

CHIRIQUÍ: El Boquete, *Pittier 2902, Davidson 544*; vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, *Allen 1370*.

7. MYRIOCARPA Benth.

MYRIOCARPA Benth. Bot. Voy. Sulph. 168. 1844.

Unarmed trees or shrubs, without stinging hairs, leaves alternate, large, toothed or rarely subentire, 3-nerved, petiolate, bearing conspicuous cystoliths; plants dioecious, rarely monoecious; staminate flowers in small, contiguous glomerules, forming slender, dichotomous spikes, the perianth 4-parted; pistillate flowers in slender, elongate, dichotomous, sub-unilateral spikes, rarely in panicles, without a perianth but subtended by 2 or 4 bractlets, the achenes stipitate or sessile.

1. Myriocarpa yzabalensis (Donn. Sm.) Killip, in Proc. Biol. Soc. Washington 40:29. 1927.

Myriocarpa longipes var. *yzabalensis* Donn. Sm. in Bot. Gaz. 16:13. 1891.

Shrub or tree, 2–10 m. high; leaves elliptic-ovate or broadly ovate, up to 35 cm. long and 18 cm. wide, acuminate at apex, rounded or slightly narrowed at base, denticulate, bearing numerous conspicuous linear cystoliths which radiate from the center of the areoles, glabrous above, glabrous, or pubescent on the nerves beneath, the petioles up to 35 cm. long; staminate spikes up to 10 cm. long; pistillate spikes very slender, pendent, up to 60 cm. long, the bractlets 2, soon deciduous, the achenes scabrid with sparse short hairs, eciliate, at length black and sometimes lustrous.

Guatemala to Panama, generally at elevations of less than 1000 meters.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 300*; Chiriquí Lagoon, *von Wedel 1411, 1445, 1505, 1692, 1699, 1886*; Columbus Island, *Skutch 5*; Almirante, *Cooper 414*. CANAL ZONE: Chagres, *Fendler 280*; Barro Colorado Island, *Shattuck 242, 494, Aviles 27, Standley 31451, 40922*; Frijoles, *Killip 3379, Standley 27572, Piper 5841*; Gatún, *Standley 27194*; Gamboa, *Standley 28400*; Obispo, *Standley 31687*; Fort Sherman, *Standley 30956*; Santa Rita Trail, *Cowell 113*; Río Indio, *Dodge & Allen 17289*; Quebrada Salamanca, *Dodge, Steyermark & Allen 16997*. CHIRIQUÍ: El Boquete, *Maxon 4946, Pittier 2878, 5157*. COCLÉ: El Valle, *Allen 4218*. COLÓN: Porto Bello, *Pittier 2487*. PANAMÁ: Río Tapia, *Standley 26215, 28277*; Río Tecumen, *Standley 29368*.

Fig. 69. *Myriocarpa yzabalensis*

PROTEACEAE

By LORIN I. NEVLING, Jr.

Trees, shrubs or rarely herbaceous, rarely dioecious. Leaves alternate, rarely opposite or whorled, simple or compound, sometimes heteromorphic, pinnately veined; estipulate. Inflorescence a head, spike or raceme, axillary or terminal, bracteate, the bracts persistent or caducous, subtending 1 to several flowers. Flowers bisexual or unisexual by abortion, monochlamydeous, cyclic, hypogynous, actinomorphic or zygomorphic. Tepals free or variously connate, petalaceous, tetramerous, valvate in bud. Stamens 4, antipetalous, the anthers dehiscing longitudinally, the filaments variously adnate to the perianth. Pistil 1, often surrounded basally by glands or a disc, often stipitate, the ovary superior, 1-carpellate, 1-loculate, the ovules 1–many, with 2 integuments, the placentation parietal or the ovules pendulous, the style 1, slender, the stigma 1, lateral or terminal. Fruit a follicle, achene, samara or drupe; seeds lacking endosperm, sometimes winged.

A family primarily restricted to the dry regions of the Southern Hemisphere, consisting of about 55 genera and 1200 species of which the majority are Australian and South African. Eight genera are represented in the New World of which two are indigenous to Panama.

A number of species are cultivated in numerous parts of Central America for their extremely showy inflorescences. At present I have no evidence of cultivated species in Panama.

The following treatment is based on a revision of the American Proteaceae by Dr. H. Sleumer (in Bot. Jahrb. 76:139–211. 1954).

a. Leaves alternate, simple or pinnately compound (heteromorphic), entire or dentate; inflorescences racemes or spikes; disc of 4 hypogynous glands; fruit a follicle, obliquely 2-valved; seeds 2, winged...................... 1. ROUPALA

aa. Leaves alternate, opposite or whorled, simple, entire; inflorescences racemes; disc cupuliform, 4-lobed; fruit indehiscent; seeds 1, exalate..... 2. PANOPSIS

1. ROUPALA Aubl.

ROUPALA Aubl. Pl. Guyan. Franc. 1:83, *t. 32.* 1775.

Leinkeria Scop. Intr. 345, *n. 1607.* 1777.
Rhopala Schreb. Gen. Pl. 1:62, *n. 144.* 1789.
Ropala J. F. Gmel. Syst. 2:225. 1791.
Rupala Vahl, Symb. 3:20. 1794.

Shrubs or trees. Leaves alternate, heteromorphic, simple or pinnately compound, dentate to entire, petiolate. Inflorescence spikes or racemes, axillary or terminal. Flowers bisexual, actinomorphic. Tepals free. Stamens inserted at about the middle of the perianth, the anthers oblong-linear, subsessile to sessile, connective sometimes broadly but briefly produced. Disc of 4 hypogynous glands. Ovary with 2 pendulous ovules, the stigma terminal. Fruit a follicle, obliquely 2-valved, with 2 winged seeds.

An American genus containing about 50 species distributed from the Isthmus of Tehuantepec southwards to Peru, Bolivia and Brazil (Rio Grande do Sul). One species is known from Panama.

1. Roupala montana Aubl. Pl. Guyan. Franc. 1:83. 1775.

Roupala pyrifolia Salisb. & Knight, in Knight Prot. 102. 1809.
Rhopala media R. Br. in Trans. Linn. Soc. 10:191. 1810.
Rhopala dentata R. Br. loc. cit. 192. 1810.
Rhopala complicata Kunth, in HBK. Nov. Gen. & Sp. 2:153, *t. 119.* 1817.
Rhopala ovalis Pohl, Pl. Bras. Ic. 1:107, *t. 86.* 1827.
Rhopala macropoda Klotzsch & Karst. in Linnaea 20:473. 1847.
Rhopala gardneri Meissn. in Mart. Fl. Bras. 5^1:83, *t. 31, f. 1.* 1855.
Rhopala martii Meissn. loc. cit. 87, *t. 32, f. 3.* 1855.
Rhopala martii var. *simplicifolia* Meissn. loc. cit. 1855.
Rhopala frondosa Rich. ex Meissn. in DC. Prod. 14:427. 1856, in syn.
Rhopala tomentosa α integrifolia Meissn. loc. cit. 428. 1856.
Rhopala boissieriana Meissn. loc. cit. 430. 1856.
Rhopala veraguensis Klotzsch, ex Meissn. loc. cit. 435. 1856, in synon.
Roupala borealis Hemsl. Biol. Centr. Am. Bot. 3:78, *t. 76.* 1882.
Roupala darienensis Pittier, in Contr. U. S. Nat. Herb. 18:228. 1917.
Roupala panamensis Pittier, loc. cit. 229. 1917.
Roupala discolor Rusby, Descr. N. Sp. Am. Pl. 12. 1920.
Roupala dissimilis Pittier, Bol. Soc. Venez. Cienc. Nat. 5:303. 1939.
Roupala repanda Lundell, in Am. Midl. Nat. 29:472. 1943.
Roupala montana var. *dentata* (R. Br.) Sleumer, in Engl. Bot. Jahrb. 76:173. 1954.

Trees to 20 m. tall, the young stems terete, ferrugineous-strigillose and glabrescent. Leaves heteromorphic; juvenile leaves pinnately compound, generally larger than the adult forms, the number of leaflets extremely variable even on a single branchlet, margin generally coarsely serrate or sometimes undulate, the veins conspicuous; adult leaves ovate, 5–12 cm. long, 2–9 cm. broad, acute or acuminate at the apex, cuneate to more or less obtuse at the base and often decurrent upon the petiole, subcoriaceous or coriaceous, ferrugineous-strigillose and glabrescent above and below, the costa plane to immersed above, emersed below, the primary lateral veins numerous, conspicuous, the margin entire, undulate to variously dentate or serrate, often repand; petiole 1–6 cm. long. Inflorescence racemose, terminal or more often axillary, multi-flowered, the rhachis 6–15 (–18) cm. long, tomentose, the flowers borne singly or in pairs. Tepals linear-oblanceolate, 7.0–8.5 mm. long, about 1 mm. broad, widely reflexed, strigillose without, glabrous within; stamens inserted about at the middle of the perianth, the anthers linear-oblong, 2–3 mm. long, 0.5 mm. broad, the filaments about 0.5 mm. long, glabrous; hypogynous glands about 0.5 mm. tall, carnose, glabrous; ovary about 1 mm. long, 1 mm. in diameter, densely strigose, the style about 3 mm. long, glabrous, the stigma narrowly clavate; pedicel to 3 mm. long, strigillose. Fruit a flattened follicle, often minutely spurred at the base, 2.5–4.0 cm. long, about 1.5 cm. broad, glabrous, the winged seeds oval, 1.5 cm. long, 0.8 cm. broad.

Distribution of the species essentially that of the genus. Flowering in January and February in Panama.

CANAL ZONE: between Corozal and Ancón, *Pittier 2630*; Ancón Hill, *Standley 26370, 26395*; without precise locality, *Hayes 1068, 1070*. CHIRIQUÍ: Sabana de la Tortuga, between El Boquete and Caldera, *Pittier 3341*; Boquete, *Davidson 1061, Pittier 3341*; David, *Seemann 1580*. COCLÉ: Penonomé and vicinity, *Williams 152*; El Valle de Antón, *Allen 2514*; between Las Margaritas and El Valle, *Woodson, Allen & Seibert 1283*.

Fig. 70. *Roupala montana*

DARIÉN: Cana, *Williams 739*; Río Pirre, *Pittier 6975*. PANAMÁ: San José Island, Perlas archipelago, Gulf of Panama, *Johnston 331, 348, 1285, 1292, 1293, 1368*; near Matías Hernández, *Standley 28949*; Taboga Island, *Standley 28001*; Tumba Muerto Road, near Panamá, *Standley 29739*; Río Las Lajas, *Allen 1600*; Punta Paitilla, *Standley 26242*.

Sleumer recognized three varieties of *R. montana* in his recent revision. One variety, var. *tomentosa*, is not treated herein, nor are its synonyms as it is restricted to Brazil. The two varieties which concern us, var. *montana* and var. *dentata*, are both represented in Panama. The character which serves to distinguish these varieties is "Folia subintegra vel undulata" for var. *montana* and "Folia bene obtuse subcrenato-serrata" for var. *dentata*. Young shoots and suckers have pinnately compound leaves, the number of leaflets is quite variable although the older generally have more than the younger, all leaflets have a serrate margin. This pinnately compound leaf is a typical juvenile form. The mature form is a simple leaf with serrate to entire margin. Although flowering is usually evidence of a mature shoot it is not necessarily evidence that the subtending leaves have attained the mature form. A few specimens show the transition from simple leaves with serrate margin to subentire or entire margin while others show that the larger stems have leaves with undulate or entire margins and the young stems have leaves which are quite serrate. It is my belief that the simple leaf with serrate margin is transitional between the compound leaf and the simple leaf with entire margin. Finally, in many collections some of the leaves are entire while others are variously serrate—needless to say this leads to the condition in which many collections and some specimens are classified in two separate varieties. Accordingly, I have not recognized var. *dentata* of Sleumer.

2. PANOPSIS Salisb.

PANOPSIS Salisb. in Knight, Prot. 104. 1809.

Andriapetalum Pohl, Pl. Bras. Ic. 1:113. 1827.
Andripetalum Schott ex Endl. Gen. Pl. 342. 1836.

Trees. Leaves alternate, opposite or verticillate, entire, simple. Inflorescences racemes, terminal or axillary, bracts small or 0. Flowers bisexual, actinomorphic. Tepals free. Stamens inserted below the middle of the perianth, the anthers oblong, connective apiculate, the filaments obvious. Disc cupuliform, 4-lobed. Ovary subsessile, with 2 pendulous ovules, the stigma terminal. Fruit indehiscent with a thick woody pericarp and 1 exalate seed.

An American genus distributed from Costa Rica southwards to Peru, Bolivia and Brazil. It contains about 11 species of which 1 is known from Panama.

1. PANOPSIS SUAVEOLENS (Kl. & Karsten, ex Klotzsch) Pittier, in Contr. Fl. Venez. 22. 1923.

Andripetalum suaveolens Kl. & Karsten, ex Klotzsch, in Linnaea 20:472. 1847.
Panopsis costaricensis Standl. in Journ. Wash. Acad. Sc. 17:164. 1927.
Panopsis mucronata Cuatr. in Lloydia 13:202, *f. 1*. 1950.

Trees to 12 m. tall, the young branches terete, ferrugineous-strigillose and glabrescent, conspicuously lenticellate. Leaves elliptic, oblong-elliptic or oblance-

olate, 4–17 cm. long, 1.5–5.0 cm. broad, obtuse, mucronulate or sometimes retuse at the apex, cuneate to obtuse at the base, coriaceous, ferrugineous-strigillose and glabrescent above and below, the costa plane above, emersed below, the primary lateral veins numerous, extremely reticulate, conspicuously emersed; petiole 2–8 mm. long. Inflorescence racemose, terminal or axillary, multi-flowered, the rhachis 6–15 cm. long, ferrugineous-strigillose, the flowers borne singly or to 4 per cluster. Tepals linear-oblanceolate, 7–8 mm. long, 0.5–0.75 mm. broad, revolutely reflexed, strigillose without, glabrous within; stamens inserted at the base of the perianth, the anthers oblong, 1 mm. long, 0.5 mm. broad, the filaments liguliform, about 6.5 mm. long, 0.5 mm. broad, glabrous; pistil long-conical, the ovary to 2 mm. long, 0.5–0.75 mm. in diameter, densely hirsute, the style 4–5 mm. long, glabrous, the stigma narrowly clavate; pedicel 4–8 mm. long, ferrugineous-strigillose. Fruit ellipsoid to ovoid, 3.5–6.0 cm. long, 2–4 cm. in diameter.

Distributed in Costa Rica, Panama, Venezuela, Colombia and Ecuador. In Panama flowering in May between 1000 and 2000 meters. According to G. White the wood ranks about 5th in Panama as a building material and is very hard and heavy. Known in Panama as *aguacatía.*

CHIRIQUÍ: Río Chiriquí Viejo, *G. White 112*; trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, *Allen 1483*; Boquete, *Davidson 630, Maxon 5133, Pittier 2954.*

Fig. 71. *Panopsis suaveolens*

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THE STRENGTHENING SYSTEM IN THE STEM OF MAIZE*

WILLIAM H. MURDY

Abstract

The system providing strength to a maize stem is described as consisting of thick-walled, lignified cells located in three distinct stem tissues: hypodermis; peripheral bundle sheaths; and sclerified ground parenchyma. Striking changes occur in the disposition of these tissues from the base of a stem to the apex, which are directly related to the plant's mode of development. Inter-racial differences in amount and arrangement of sclerotic tissue are described, and contrasted with the strengthening systems of *Euchlaena* and *Tripsacum*. William H. Murdy, Emory University, Atlanta 22, Georgia.

Introduction

The species *Zea mays* is characterized today by an almost overwhelming range of variability; a consequence attributed in part to its unique history in association with ethnic groups of man in the New World, and in part, to former introgression with the genus *Tripsacum* and the present ability to exchange germ plasm with *Euchlaena* (teosinte; a genus of putative hybrid origin between *Zea* and *Tripsacum*).

The concept of race has been advanced as a step toward a natural classification of this variability. Anderson and Cutler (1942), largely responsible for the evolution of this concept, defined a race loosely as a "population of maize plants differing from other groups by a great number of genes and sharing enough characters in common to be easily recognized as a distinct group".

For the past several years, the Rockefeller Foundation in collaboration with Latin American countries has been performing the arduous task of classifying indigenous races of maize in Central and South America. The character of scleroticness, as expressed by features such as stalk stiffness, the coarseness of leaves and cob induration, is one of many polygenic characters by which races of maize have been found to differ. The magnitude of tissue induration is frequently accepted as evidence of teosinte or *Tripsacum* contamination, since highly sclerotic plants often exhibit other plant characters regarded as "tripsacoid" in nature (Wellhausen, 1952). Moreover, segregates from maize-teosinte crosses often

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possess an inordinate degree of tissue induration (Mangelsdorf and Cameron, 1942). Galinat et al. (1956) state that "extensive experiments with maize-teosinte hybrids have demonstrated that genes responsible for lignification occur on many, if not all, of the chromosomes of teosinte".

The character of sclerification, when properly evaluated, should add materially to our knowledge concerning the origin of modern maize and its past and present relationship with *Euchlaena* and *Tripsacum*. The present study was undertaken in order to shed light on the following basic questions: (1) What stem tissues become sclerified to make up the strengthening system and how do these tissues differ in amount and arrangement from the base of a stem to its apex? (2) What is the range of variability within and between races of maize in respect to the strengthening system? (3) What relationship exists between the strengthening system of maize and that of *Euchlaena* and *Tripsacum*?

One of the foremost requisites of good breeding stock is an ability to stand up well and contribute a fair share of stalk-stiffness in crosses. Several anatomical studies, based on the lower internodes of inbred lines, have established a correlation between lodging resistance and the nature of sclerotic tissue (Magee, 1948; Hunter and Dalbey, 1937). The results of these investigations are valuable to the corn breeder, but have only an indirect bearing on the nature of sclerotic, strengthening systems in vigorous open-pollinated races.

Materials and Methods

Six maize races were selected from the "Standard Exotics" described by Anderson and Brown (1951), which represent the extremes of variation in *Zea mays* growable in the corn belt. Many plants of each race were grown under essentially uniform field conditions at the Pioneer Hi-Bred Corn Company, Des Moines, Iowa. Following is a brief description of each race.

Gourdseed (Brown and Anderson, 1948)—An old southern dent variety typical of the kind of maize commonly grown in southeastern United States in colonial times. This particular stock was collected by Dr. W. L. Brown in 1946 at Grapevine, Texas. Plants are generally tall, having many internodes, few tillers, and greatly condensed ears and tassels. Chromosome knob numbers medium high (5–7); plants mature slowly (approximately 94 days from planting to silk in Iowa).

Northern flint (Brown and Anderson, 1947)—Representative of the maize once grown almost exclusively in the northern and eastern sectors of the United States until superseded by early corn-belt varieties. Plants vary somewhat throughout their range, but share many features in common including low chromosome knob numbers (0–2), eight-rowed ears, few, but long internodes (those above the ear not decreasing in length as in the case of Gourdseed), several tillers shorter in height than the main stem, and a rapid growth rate (from planting to silk in Iowa takes approximately 66 days).

Argentine pop (Anderson and Brown, 1951)—A small-eared, prolific pop corn race of Paraguay and Argentina. Unlike the other five races, Argentine pop has not likely been contaminated by either North American *Tripsacum* or teosinte. Furthermore, its ear is closest to the concept of prehistoric South American maize

based on archeological evidence. It grows slowly in Iowa and at maturity consists of a main shoot with many short internodes relatively equal in length, plus a few tillers shorter than the main culm. Planting to silk requires approximately 105 days.

Chapalote (Wellhausen, 1952)—A pop corn race grown in the coastal lowlands of northwestern Mexico. Plants are "tripsacoid" in appearance in the possession of several long, ear-bearing tillers approaching in height the main shoot, long internodes, and long narrow leaves. Wellhausen classified this race as a primitive, indigenous pop corn with little evidence of teosinte contamination. Chromosome knob number is variable; the average is approximately six. About 90 days are required from planting to silk in Iowa.

Papago (Anderson and Cutler, 1942)—Seed of this race was obtained from the Papago Indians in the desert south of Tucson, Arizona. It is typical of the maize grown by desert-dwelling Indians and similar to archeological maize grown by the prehistoric Basketmakers—the first agriculturalists of this region to leave a record (Anderson and Blanchard, 1942). Its habit resembles that of Chapalote; long ear-bearing tillers, long internodes, and long narrow leaves. Chromosome knob number is medium high and growth rate quite rapid (approximately 77 days from planting to silk in Iowa).

Zapalote chico (Wellhausen, 1952)—An extremely sclerotic race grown in the coastal lowlands of southern Mexico. Plants are coarse and indurate, lack tillers, and have many short internodes above the ear. Chromosome knob number is high (12–16) and Wellhausen considers this race to be highly contaminated with teosinte germ plasm. It matures rapidly in its native habitat and is comparatively independent of day length when grown in Iowa. Planting to silk requires approximately 81 days.

Six plants of Florida teosinte (*Euchlaena mexicana*), from a commercial source, were used in this study; two were grown in Iowa and four in Florida. Plants from two separate clones of *Tripsacum dactyloides* were sampled; one growing in Iowa and the other located in St. Louis, Missouri. A single plant of *Tripsacum lanceolatum* collected in Guatemala by Dr. E. Anderson was also included in this study.

Just after anthesis, 15 plants of each maize race were selected in an attempt to adequately sample the range of morphological variability within races. Plants were collected when completely mature and subsequently subjected to morphological and anatomical analysis. In making anatomical sections of desiccated stems, internodal discs about 2 cm. long were boiled in water, with aerosol added, for approximately 4–5 hours; placed in 50 percent alcohol overnight; sectioned with a sharp razor; stained with safranin and fast green; and permanently mounted in piccolyte, a synthetic mounting medium.

Maturation of a Maize Stem

The stem of maize can be looked upon as a series of alternating segments, or phytomers (Evans and Grover, 1940). Each phytomer is made up of an internode, with a leaf at its upper end and a bud at its base. Final maturation of a phytomer begins in the leaf blade, passes down the leaf sheath and finally down the internode

below. Successive phytomers, however, mature acropetally up to, but not including, the tassel peduncle, which together with its tassel does not await the ascending wave of maturation, but matures relatively early at a time when the internodes immediately below are still immature. Normally there is no leaf associated with the tassel peduncle, thus, internodal tissue maturation begins in the upper portion of this internode. By measuring internode lengths of genotypically uniform hybrid plants at various stages of maturity, one is able to obtain a picture of the ontogenetic pattern of stem development (fig. 1). Note the plant examined ten weeks after planting; it is still relatively immature, nevertheless, the leafless peduncle is already 11 cm. long, almost half its assumed maximum length, while the two internodes immediately below, associated with leaves, are merely 2 cm. in length, only one-ninth their assumed maximum length at maturity.

A similar pattern of maturation was reported by Prat (1935) for stems of *Secale cereale*. He noted that the terminal internodes bearing the inflorescence elongated more rapidly than the subterminal internode. By subjecting these two internodes to mechanical stress, he found the uppermost to be more resistant. He concluded that rapid maturation accompanied rapid elongation and that both processes occurred faster in the terminal internode than in the one below.

It is likely that the maturation of a maize stem conforms to a pattern widespread in the Graminae. Knowledge of this pattern is essential to an understanding of maize stem anatomy, for the rate at which an internode grows and matures has a direct bearing on its internal structural features.

Strengthening Tissues in a Maize Stem

In herbaceous monocots generally, mechanical stem strength is provided by thick-walled sclerotic tissue. The process of cell sclerification entails the deposition of a thick, cellulosic secondary wall and subsequent impregnation of primary and secondary walls with lignin. Tissues that contribute most to the strength of a maize stem can be classified in three categories: (1) sclerenchyma associated with vascular bundles; (2) hypodermal sclerenchyma; (3) sclerified parenchyma.

Vascular bundle sclerenchyma. A maize stem in cross-sectional view (plate VI, D) shows a scattered arrangement of vascular bundles surrounded by parenchymatous ground tissue. Those bundles near the periphery of the stem are crowded, small and generally provided with heavy sclerotic sheaths, whereas the more central ones are widely-spaced, larger in size, and lack massive sheaths. The presence of two distinct vascular systems in maize has previously been reported. Both Esau (1943) and Cutler and Cutler (1948) reported two systems in the stem. The latter authors referred to the outer system as the "peripheral" and the inner as the "central". Two quite dissimilar systems have also been noted in the ear (Lenz, 1948; Laubengayer, 1949; Reeves, 1950) and tassel (Kumazawa, 1940).

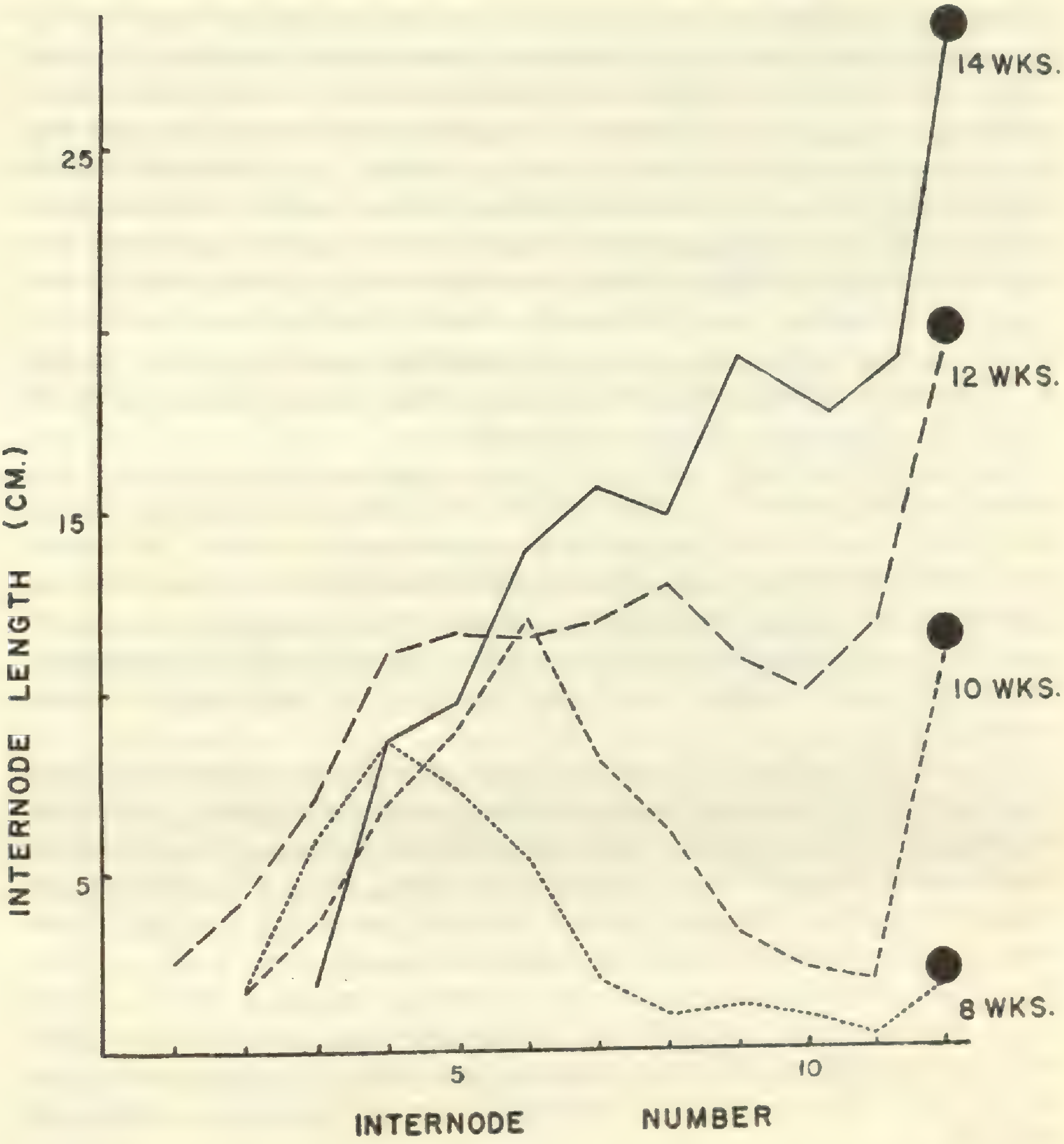

Fig. 1. Internode diagrams of genotypically identical plants measured at intervals of 8, 10, 12, and 14 weeks after planting. Successive stem internodes elongate acropetally except for the tassel peduncle.

The leaves of maize are vascularized by large, early-maturing bundles and smaller late-forming bundles which alternate with the larger ones. At a node, the large leaf bundles pass some distance into the stem at a right angle before assuming a vertical or oblique course down through the internode below. Ontogenetically, the large bundles originate at the node and simultaneously differentiate in two directions; up into the leaf and down through the internode before either of these organs have completed their elongation. Only when acropetal differentiation of these large bundles reaches the tip of the leaf blade, do the small alternating

bundles begin to differentiate basipetally in the distal part of the leaf blade, developing at a time when most elongation of leaf and stem has been completed (Sharman, 1942). At a node these small bundles pass into a ring of vascular tissue, formed by the lateral anastomosis of peripheral strands from the internode above, and their sheaths become merged with those of the ring bundles. Just below the node the peripheral ring of vascular tissue breaks up into distinct bundles, which pass down the periphery of the internode below. Hence, the majority of peripheral stem bundles, which play a leading role in support of the stem, are prolongations of late-maturing leaf bundles. Some of the smallest bundles found in the peripheral region of the stem have an even later origin in the intercalary meristem region at the base of a leaf sheath. Esau (1943) illustrated the origin of such bundles within the massive sheaths of large, early-maturing bundles.

All vascular bundles of appreciable size are associated with a sheath of protective fiber cells, heaviest at the protophloem and protoxylem poles (plate VI, B). Esau (1943) described the ontogeny of the vascular bundle in maize. She pointed out that the fibers of the sheath originate mainly from the procambium which also gives rise to the vascular tissue itself; in addition, tissue adjacent to a bundle may contribute cells to the sheath in its somewhat advanced stage of development. The amount of such accretion varies with the size of the bundle and its location in the plant.

The vascular bundles with associated sheath sclerenchyma comprise the "backbone" of the skeletal structure supporting the stem of a maize plant. In the form of strengthening rods passing discretely through parenchymatous ground tissue the bundles contribute little to the support of the plant. It is only when they are arranged in various structural patterns that their mechanical function is most effective. The peripheral bundles with prominent sheaths, may, by the sclerification of inter-bundle parenchyma, form a continuous supporting cylinder, at least in the lower internodes (plate VI, A). Similar peripheral bundles in upper internodes are frequently welded to the epidermis by a bridge of sclerotic tissue derived in part from the bundle sheath and partly from the hypodermis (plate VII; D, E. F).

Hypodermis. Immediately beneath the epidermis of a maize stem is a zone of thick-walled, elongate fiber cells (plate VI, A). This tissue, commonly known as a hypodermis, is lacking or poorly developed in lateral and foliar organs. Frequently the hypodermis is very thick in its radial dimension and makes a substantial contribution to the strength of certain parts of the stem.

Ontogenetically, the subepidermal meristematic cylinder which gives rise to the hypodermis probably originates from the "flank meristem" of Ledin (1954). Popham (1951) refers to this histogen as a peripheral meristem forming a cylinder between the protoderm, which gives rise to the epidermis, and central meristem, which develops into pith and procambial strands. In ontogeny, parenchyma cells underlying the epidermis undergo longitudinal divisions and as the internode elongates, these initials do not undergo transverse division, but grow rapidly in the

axial direction resulting in the development of long narrow fibers (Hayward, 1938). Hypodermal fibers isolated from plants of the race Papago average 1.2 mm. in length and are 100× longer than broad. During growth, the tips of the fibers push past one another resulting at maturity in a very strong non-storied peripheral cylinder.

Accentuated development of hypodermal sclerenchyma is found just above the point where a leaf or lateral branch departs from the main stem. This fact may have a significant bearing on the problem of intense sclerification of the cob rachis where the internode above each lateral branch (spikelet pair) is greatly abbreviated.

Sclerified parenchyma. Parenchymatous tissue in the outer region of a stem frequently becomes thick-walled and lignified to an extent that differs greatly among internodes of a single plant. When well-developed, the sclerotic parenchyma takes the form of a thick, subepidermal, sclerotic cylinder pervaded by peripheral vascular bundles (plate VII; A, B).

Changes in the Strengthening System of an Individual Stem

Structural changes in anatomy from one internode to another have not been described for maize, but are known in other grasses. Prat (1935) found internodes to vary in their ability to withstand mechanical pressures. The lower internodes were strongest in this respect with resistance diminishing acropetally. Athanassoff (1928) described the anatomy of successive internodes of a wheat culm. He found that internodes differed in the relative amount and arrangement of sclerenchyma, parenchyma, and vascular tissue. He also noted that internodes differed in respect to their time of maturation.

Anatomical sections of six internodes from the stem of a single plant are pictured in plate VII. The principal structural differences among internodes include the following: variation in size, shape, and sheath development of peripheral vascular bundles; differences in the relationship of these outer bundles with subepidermal sclerenchyma; and, changes in the extent of hypodermis and sclerified parenchyma development.

Peripheral vascular bundles. The peripheral bundles are very small in the lowermost internode (plate VII, A), but increase in size acropetally. In the internodes below the ear (plate VII; A, B, C) peripheral bundle sheaths, though massive, show very little centrifugal development, and between sclerenchyma at the protophloem end of the bundles and sclerenchyma of the hypodermis is a zone of thin- or thick-walled parenchyma. Peripheral bundles in the internodes above the ear (plate VII; D, E, F) are large in size and rhomboid in shape. These bundles have a much greater development of sheath sclerenchyma at the protophloem pole which, being confluent with the hypodermis, results in the formation of sclerotic "bridges" connecting the peripheral bundles to the epidermis.

The small, peripheral bundles in the lower internodes (plate VII; A, B) evidently matured after these internodes had ceased to elongate. They have little protophloem and protoxylem and are relatively unstretched, as evidenced by the

lack of a protoxylem lacuna (Esau, 1943). Their complete dissociation from the hypodermis and sub-epidermal parenchyma infers that their development in the internode occurs after these outer stem tissues have matured. In the internode just below the lowest ear (plate VII, C) peripheral bundles are somewhat larger than in lower internodes. In addition, they possess protoxylem and the middle bundle is somewhat stretched. Therefore, up to this point, there is an acropetal narrowing of the time lag between the maturation of the outer internodal tissues and the peripheral bundles. From the next internode on into the tassel the anatomy of the stem undergoes a striking change (plate VII, D). In these upper internodes, peripheral bundles differentiate prior to the completion of internode elongation and at a time when the outer tissues of the internode are still immature and capable of further division and elongation. As a result, these bundles are large, with well developed protoxylem and protophloem, and a large protoxylem lacuna. Moreover, bundle sheaths are well developed at the protophloem pole and confluent with hypodermal sclerenchyma. Except for size, the peripheral bundles in the peduncle and tassel (plate VII; E, F) are comparable to those of the internodes immediately below and are similarly bridged to the epidermis.

The structural variation of vascular bundles in the corn stem described above is attributable to differences in the relative period of development and maturation of outer stem tissues and the vascular bundles descending through them from leaves above. Starting with the lowermost internodes where the peripheral bundles develop some time after the completion of internode elongation, there is a gradual change in this relationship whereby the development and maturation of the two tissues is progressively more closely approximated. At a point where the lowermost ear is borne, the development and maturation of the two tissues is coincident. Sharman (1943) has pointed out that the time taken for the internode to complete its development increases with the maturity of the plant. He noted that "in the upper internodes there may be a lapse of four or more plastochrones between the full expansion of the lamina and internode." In other words the development and maturation of leaves with their included vascular strands, occurs at a fairly uniform rate acropetally, whereas the maturation of tissue in successively higher internodes progressively slows down.

An internode pattern of this plant (fig. 4, lower right) shows that the lower internodes (aside from the first two above the ground), which on the basis of anatomy were found to mature rapidly, are elongate, whereas the slower-maturing, upper internodes have relatively short lengths. Consequently, the changes in the length of internodes coincides with the changes in structural anatomy and both reflect the particular growth behavior characteristic of this plant.

Hypodermis. The greatest development of hypodermal sclerenchyma occurs in the middle internodes of the plant (plate VII; C, D), diminishing in extent below (plate VII; A, B) and above, where it is found only opposite bundles in peduncle and tassel internodes (plate VII; E, F). The lower internodes and tassel mature more rapidly than internodes between and those just beneath the peduncle are the slowest to mature. It is precisely in these short, upper internodes, having the slowest rate of maturation, that the hypodermis has its greatest development.

Sclerified parenchyma. In the upper internodes intervening parenchyma between peripheral bundles is firm, but relatively thin-walled and unlignified. Intense sclerification of ground parenchyma occurs in internodes quite low on the plant (plate VII; A, B). The lower internodes are the earliest to originate and have a longer period of time to deposit cell wall material. In addition, there is a great basipetal flow of sugar through these lower internodes especially in the early stages of the plant's growth. The upper internodes have a longer period to differentiate fiber cells, but a shorter period for these cells to deposit cell wall material prior to final desiccation. Furthermore, after fertilization of the ear a great amount of sugar is channeled into the developing kernels causing a drain on the availability of sugars required for the synthesis of cellulose in late-developing internodes.

Racial Variation in the Strengthening System of Maize

Hypodermis. In all races examined (except Argentine pop) hypodermal tissue develops to its greatest extent in the upper stem internodes between ear and tassel. It is suggested that prolonged activity of the peripheral meristem in these upper, slower-maturing internodes results in the differentiation of a great number of hypodermal fiber cells prior to tissue maturation. Races differ, however, in the extent of hypodermal tissue development, which may in part result from a dissimilarity in growth behavior. For example, plants of the race Gourdseed consistently have a thicker hypodermis (greater radial number of fiber cells) than do plants of the race Northern flint (plate VIII; B, D). As a race, however, Gourdseed is characterized by having a slow rate of growth and a series of short slow-maturing internodes above the ear shoot—the region of greatest hypodermal development in all races. Northern flint plants, on the other hand, have a rapid growth rate and the upper internodes are long and relatively quick to mature. Therefore, when comparing the potential ability of these two races to produce hypodermal sclerenchyma, their respective growth patterns must not be overlooked. Although in most races the upper internodes invariably mature more slowly than middle and lower ones, the race Argentine pop is characterized by a very uniform rate of growth resulting in all internodes being short and relatively slow to mature. In plants of this race middle internodes of the stem show the greatest extent of hypodermal development (plate IX, B).

Growth rate does not wholly account for the hypodermal differences observed among races. Papago, the race with the thickest hypodermis (plate VIII, A), is one of the most rapid to mature. In this race, however, the unusually heavy hypodermis is associated with deep-lying peripheral vascular bundles and both features may have definite selective value for such a semi-xerophytic race in diminishing the extent of water loss from stem tissues.

The amount of hypodermal tissue development in plants of a particular race is fairly uniform. Where intra-racial differences do occur, they are accompanied by changes in the overall scleroticness of the plant. When the width of the hypo-

dermal zone is measured in the internode of its greatest development, races of maize analyzed line up from greatest to least in the following manner: Papago (plate VIII, A); Gourdseed (plate VIII, B); Zapalote chico (plate VII, D); Chapalote (plate VIII, C); Argentine pop (plate IX, B); Northern flint (plate VIII, D).

Hypodermal tissue is not a prominent feature in the stems of teosinte plants examined (plate VIII, E). *Tripsacum* likewise lacks an appreciable development of continuous hypodermal tissue. The strengthening system of *Tripsacum,* however, is characterized by separate, peripheral strands of procambial tissue which at maturity form sclerotic connections between peripheral vascular bundles and epidermis. Thin-walled chlorenchymatous tissue lies between adjacent girders.

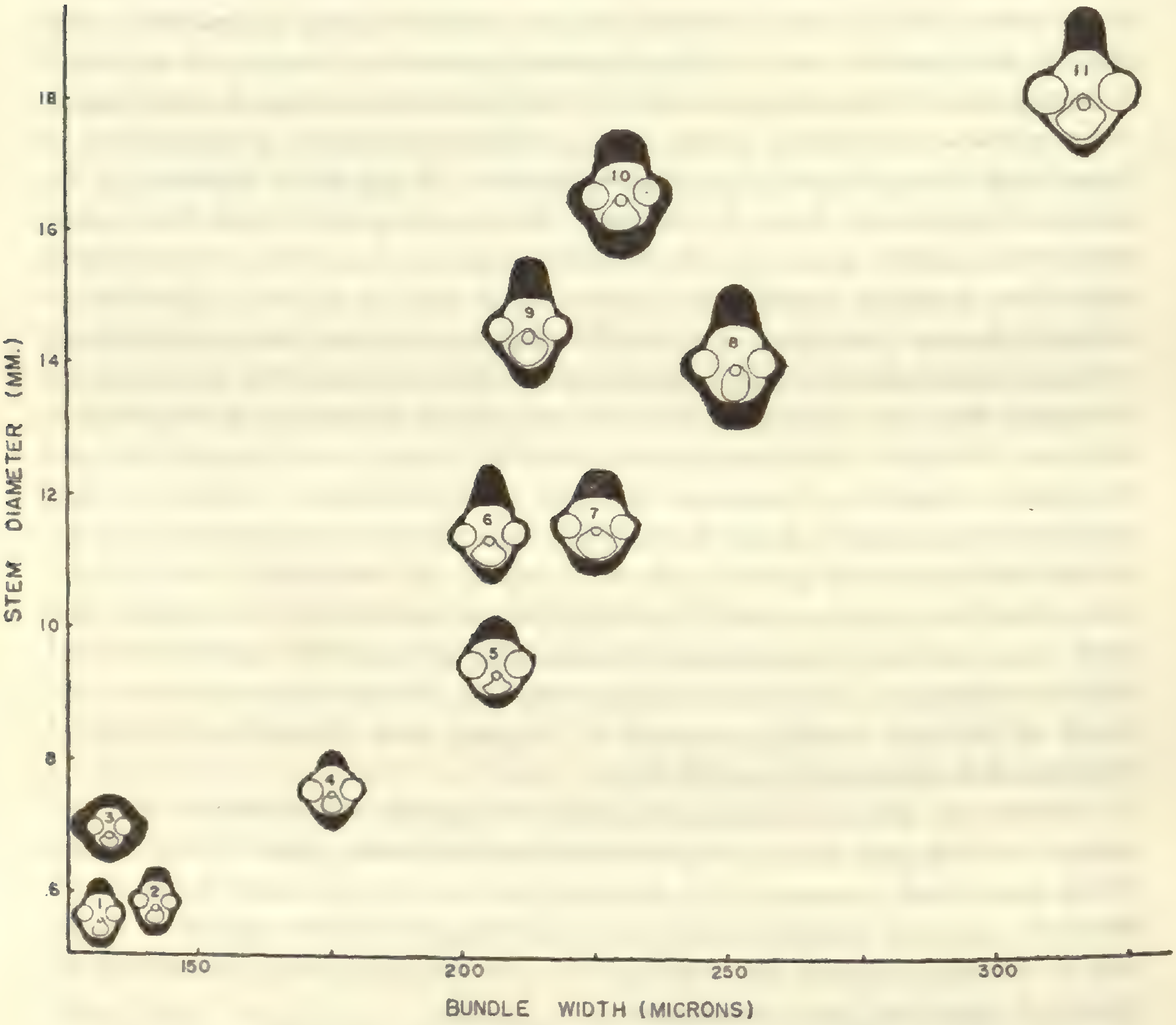

Fig. 2. Pictorialized scatter diagram to show the relationship of bundle width to stem diameter and amount of bundle sheath sclerenchyma for six races of maize plus teosinte and two species of *Tripsacum.* 1, *Tripsacum dactyloides*; 2, Teosinte grown in Florida; 3, *Tripsacum lenceolatum*; 4, Teosinte grown in Iowa; 5, Argentine pop; 6, Gourdseed; 7, Chapalote; 8, Northern flint; 9, Zapalote chico; 10, Papago; 11, Gourdseed (extreme plant).

Vascular bundles. The vascular bundles found in any cross section of a corn stem vary in size, shape, and also in their amount of associated sheath sclerenchyma (plate VI, D). Just inside the outer ring of heavily sclerotic bundles is a zone of strands, intermediate in character between the small, often reduced peripheral strands and the large, greatly stretched central ones. This ring of bundles is most easily discerned in the upper internodes of a corn stem and within a particular internodal cross section bundles are remarkably uniform in all their features. Determinations of bundle size were carried out on five such bundles (one appears on plate VI, B) from the fourth internode below the peduncle in each plant studied. Bundle size refers only to the dimensions of the vascular tissue within the bundle sheath.

Vascular bundle size varies somewhat among plants of a single race, but to a greater extent from plants of one race to those of another. Nevertheless, in both instances there exists a strong correlation between the diameter of a particular internode and the size of its contained bundles. The relationship of bundle size to stem diameter for five races of maize plus teosinte and two species of *Tripsacum* is diagrammed in fig. 2. Each symbol represents the average bundle dimensions of a race with the relative amount of sheath sclerenchyma in black. The races Papago (10), Northern flint (8), Zapalote chico (9), and most Gourdseed plants (6) show a heavy development of sheath sclerenchyma in proportion to bundle size, especially when compared with Chapalote (7), Argentine pop (5), and teosinte (4). Relative to bundle size, sheath sclerenchyma is weakly developed in teosinte, greatly developed in *Tripsacum dactyloides* (2), and massive in *Tripsacum lanceolatum* (3).

Peripheral stem bundles become progressively smaller and more reduced in successively lower internodes. This change is accompanied by an increase in their associated sheath sclerenchyma. Moreover, the walls of the fiber cells constituting the bundle sheath become thicker in successively lower internodes.

All plants of the race Zapalote chico conform to the structural pattern shown by the plant pictured in plate VII in that most of the peripheral bundles of upper internodes are connected to the epidermis by a sclerenchymatous bridge. A similar pattern, however, is not found in all races of maize. For bridging to occur in any plant internode it is necessary that the peripheral bundles lie close to the epidermis and that sufficient bundle sheath sclerenchyma develops at the phloem poles prior to the maturation of sub-epidermal tissue.

Papago has deep-lying peripheral bundles and though heavily sclerotic, none are bridged to the epidermis in any stem internode. Plants of the race Chapalote vary in their incidence of bridging, but the variation is correlative with peripheral bundle distance from the epidermis. On the other hand, proximity of peripheral bundles to the epidermis is not solely responsible for the incidence of bridging, either in a single stem or in a race. For example, peripheral bundles in all internodes of a teosinte stem lie close to the epidermis, but bridging only occurs in the peduncle and upper one or two internodes (plate X, A). In respect to races, all

peduncles of Zapalote chico plants studied have over fifty per cent of their peripheral bundles bridged to the epidermis, even when these bundles lie 150 microns from the epidermis (a distance greater than that of unbridged Chapalote plants). On the other hand, the peripheral bundles in the stems of Argentine pop lie relatively close to the epidermis, but are unbridged.

Considering only the phenomenon of bridging in maize, teosinte and *Tripsacum*, the following classification can be made.

1. *No bridging in any internode of the plant.* This condition is found in Argentine pop (plate IX; A, B) and in the North American pop corn race, Ladyfinger.
2. *Bridging in the tassel, tassel peduncle and 2–3 internodes below.* Northern flint, Zapalote chico (plate VII; A–F), Gourdseed (plate IX; C, D), Chapalote, and teosinte (plate X; A, B.)
3. *Bridging in all plant internodes. Tripsacum dactyloides* (plate X; C, D) and *Tripsacum lanceolatum.*

The lack of bridging in Argentine pop may be due to the distance of peripheral strands from the epidermis, paucity of sheath sclerenchyma, or both. It is possible, however, that it is in part a result of a particular pattern of growth, basically different from both *Tripsacum* and the races of maize which exhibit bridging. Argentine pop plants have a very slow growth rate and at maturity each plant consists of a great number of short internodes differing little in length (fig. 4). The longest internode occurs in the lower one-third of the plant. Beyond this point successive internodes gradually diminish in length up to the tassel peduncle, which itself is seldom longer than the internode next below and barely, if at all, exserted beyond the uppermost leaf sheath. Peripheral bundles are uniformly small and unstretched throughout the length of the plant. This infers that in each internode the peripheral bundles mature after the completion of tissue elongation. Hence, in all internodes of the stem, internodal tissue and peripheral bundles mature at a rather uniform rate, the former keeping ahead of the latter.

The presence of bridging in upper plant internodes but not in those below has been described for Zapalote chico (plate VII) and attributed to an extreme retardation in the rate of maturation of internodes above the ear shoots. A similar change occurs in the slow-maturing race Gourdseed, which like Zapalote chico, is characterized by a series of very short internodes between the ear and tassel.

Northern flint and teosinte grow rapidly and the upper internodes slow down only slightly in their rate of growth and maturation (fig. 4). As in Gourdseed and Zapalote chico, the peduncle and upper one or two internodes exhibit bridging. Such bridging is likely the result of a speeded-up maturation of peripheral bundles coupled with a slight decrease in stem tissue maturation, for the upper 2–3 leaves are always very much shorter than those below. Hence, the peripheral bundles have a much shorter distance to differentiate before reaching the stem. In the case of Zapalote chico, the change in peripheral bundle configuration is abrupt; in Northern flint and teosinte it is gradual. For example, in one plant of teosinte,

eighty percent of peripheral bundles in the peduncle were bridged to the epidermis, fifty percent in the internode below, fifteen percent in the next lowest internode and zero percent in the one below that.

In the genus *Tripsacum,* the formation of girder sclerenchyma is an outstanding feature of its strengthening system, occurring throughout the length of the plant (plate X; C, D). It is also a common structural arrangement in grasses generally. Hayward (1938) stated that stems so constructed have a "continuous zone of hypodermis variable in thickness within the epidermis and enclosing longitudinal bands of chlorenchyma". More precisely, the outer portion of such a stem consists of a parenchymatous cortex, regularly interrupted by girders of sclerotic tissue, which link peripheral bundles with the epidermis (plate X, C). Only in lower internodes do peripheral bundles become connected laterally by the sclerification of parenchyma lying between them (plate X, D). In these lower internodes the longitudinal bands of parenchyma appear to be "imbedded" in a continuous mass of hypodermal sclerenchyma, but actually, the isolation is circumscribed laterally by girder sclerenchyma and within by sclerified parenchyma. Percival (1921) stated that "a portion of the outer face of the chlorenchyma bands is always in immediate contact with the epidermis". This is true for the upper internodes of *Tripsacum* but in lower internodes the epidermis is underlain by a single layer of large hypodermal cells.

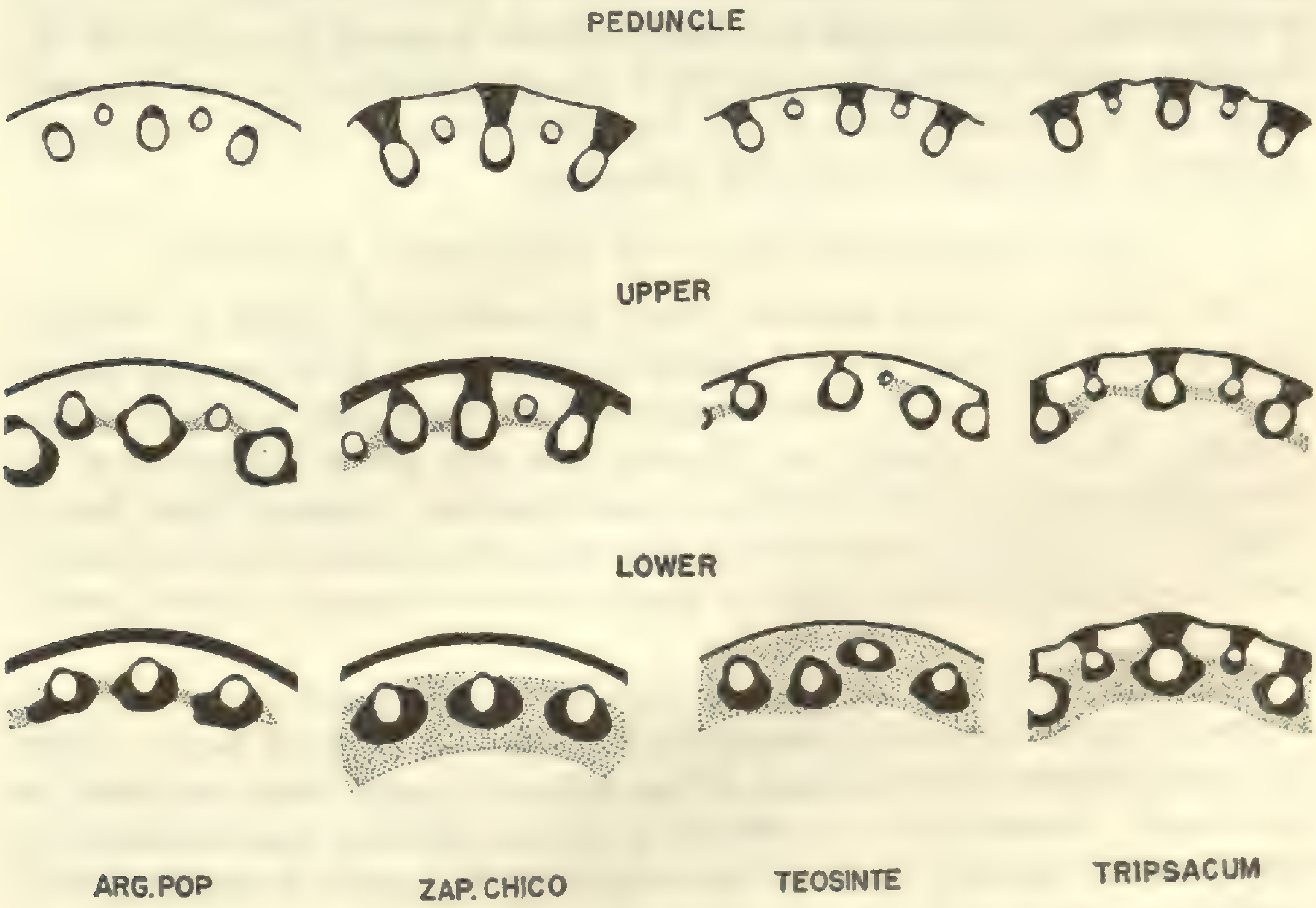

Fig. 3. Representative drawings of internodal cross-sections to show the variation in bridging within peduncle, upper internode, and lower internode in Argentine pop, Zapalote chico, Teosinte, and *Tripsacum*. Sclerotic fiber tissue in black; sclerified parenchyma stippled.

The peripheral bundles in *Tripsacum* lie close to the epidermis and their maturation in the stem either coincides with that of outer stem tissue or the procambium itself extends to the epidermis. *Tripsacum* has a rapid growth rate and at maturity consists of a relatively small number of extremely long narrow internodes culminating in an even longer peduncle (fig. 4). Maturation processes in this genus must be investigated before an attempt is made to compare its pattern of growth with maize.

In summary, the strengthening system found in the lower internodes of most maize races studied parallels the condition found in an entire Argentine pop plant. The upper internodes, however, have a structure resembling that of *Tripsacum.* Figure 3 diagrammatically represents the basic differences in bridging described in this section.

Sclerified parenchyma. In all plants examined the lower the internode the wider the zone of sclerified parenchyma. In lower internodes sclerified parenchyma forms a radially thick, sclerotic cylinder traversed by vascular bundles (plate VII, A). Higher up (approximately 8 internodes below the tassel peduncle) it is found chiefly between peripheral vascular bundles (plate VI, B; plate IX, B, D; plate X, B, D). In the fourth internode below the tassel peduncle interfascicular sclerenchyma is found only in Papago (plate VIII, A) and in the tassel peduncle sclerified parenchyma is never found (plate IX, A, C; plate X, A, C).

A high degree of intra-racial variation occurs in regard to the extent of parenchyma that becomes sclerified, however, races which consistently were weak in the development of sclerified parenchyma include Argentine pop (plate IX, B), Chapalote, and Northern flint, whereas it was always prominent in Gourdseed (plate IX, D), teosinte (plate X, B), Papago, and Zapalote chico. Its greatest development was found in *Tripsacum* (plate X, D).

The Strengthening System of the Lateral Ear Shoot

The lateral ear-bearing shoot, or shank, is anatomically similar to the main stem except for its lack of a well-developed hypodermis and the presence of numerous small, peripheral bundles, which originate in the excessively wide leaf sheaths or husks. The very sclerotic race Zapalote chico does have a hypodermis in the shank and at maturity internodes have a smooth surface. In other races, there is little or no hypodermis present and with desiccation the collapse of parenchymatous tissue beneath the epidermis results in the formation of externally visible grooves and ridges.

In addition to sclerotic tissue, shank strength depends on such factors as length of shank, length of internodes, diameter of internodes and weight of the ear. There is a great difference in the anatomy of internodes of a single shank depending on their length. Consequently, it is difficult to compare the short shank internodes of Gourdseed, for example, with the very long shank internodes of Northern flint. Furthermore, the amount of sclerenchyma in a shank bearing a fertilized ear is much greater than in one which bears an unfertilized ear.

Vascular bundles in the shank are generally provided with a heavy sclerotic sheath, which frequently prevents crushing of vascular tissue when arching or bending occurs. The overall strength of the shank, however, depends on the strength of tissue between the bundles or the extent of ground tissue sclerification.

The races Zapalote chico and Papago, very sclerotic in respect to their stems, have a great amount of sclerified parenchyma in their shank internodes. In plants of these two races, shanks varied in length from 7–28 cm., but all were erect at maturity. Plants of the race Gourdseed characteristically have short shanks (6–16 cm.) and their internodes have a fair amount of sclerified parenchyma. Nevertheless, all shanks of this race were bent or broken due in large measure to the combination of a very heavy ear and narrow lower internodes.

Both Northern flint and Chapalote have relatively long shanks (11–32 cm.).

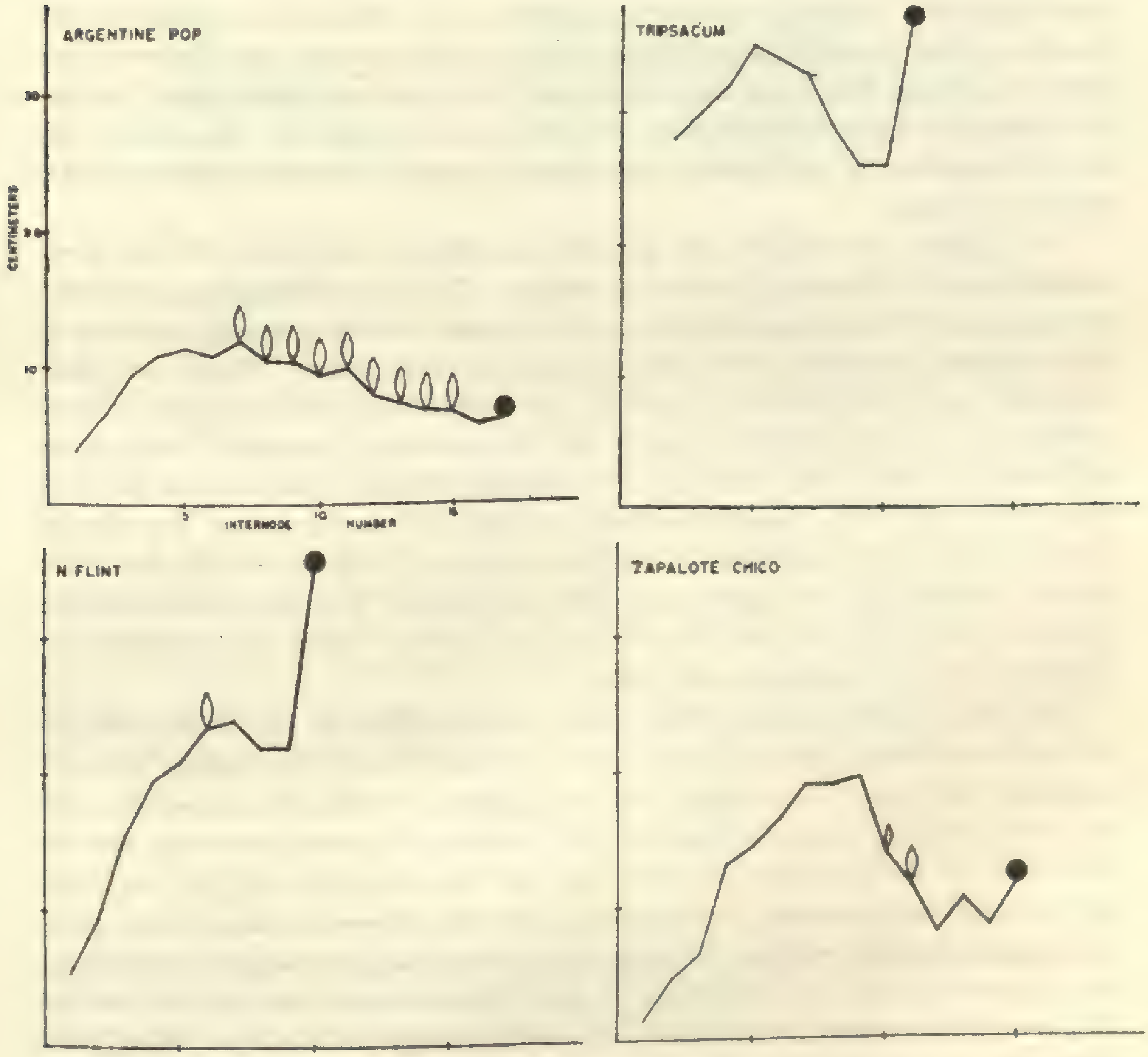

Fig. 4. Internode diagrams which typify the pattern of growth found in the races Argentine pop, Northern flint, and Zapalote chico, and the species *Tripsacum lanceolatum*.

At maturity all shanks of Chapalote plants were erect, whereas shanks of Northern flint plants were either bent or broken. The long shanks of Northern flint have few internodes and grow rapidly, while on the contrary, those of Chapalote have many internodes and a slow rate of growth. Anatomically, shank internodes of Chapalote have a wide zone of sclerified parenchyma, but there is practically none of this tissue present in the internodes of Northern flint. Since the stems of both races are quite similar in respect to sclerenchyma, the greater shank strength in Chapalote is probably due to the much longer period cells are able to deposit wall material before final maturation and desiccation.

Argentine pop has small ears borne on relatively short shanks which have many internodes, grow slowly and have fairly strong interbundle connections.

Conclusion

The tissue which strengthens and supports a maize stem can be subdivided into three categories: long fibers of the hypodermis; short fibers of peripheral bundle sheaths; and thick-walled, lignified parenchyma. The amount and disposition of these three tissues differs in a single stem and the manner of change from the base of a plant to its apex is dependent on the plants growth behavior. As a result, the relative importance of each tissue in contributing strength changes in different parts of the same stem.

The greatest sclerification of ground parenchyma takes place in the lower internodes—the earliest on the plant to mature. This tissue diminishes acropetally and occurs only between peripheral bundles in upper middle internodes and not at all in the tassel, peduncle and the two to three internodes below. Middle and upper internodes are strengthened principally by hypodermal sclerenchyma, which develops its greatest radial thickness in the slow-maturing internodes between ear and tassel peduncle. The importance of peripheral bundle sclerenchyma increases acropetally. In middle internodes these bundles are interconnected laterally by sclerified parenchyma and form a continuous sclerotic cylinder within the hypodermis. Higher up, the lateral connections are weaker but sheath sclerenchyma developing at the phloem end of a bundle may connect with the hypodermis or epidermis forming a subepidermal girder.

The basic growth pattern of all maize races is similar in that elongation and maturation of leaves and internodes occurs acropetally with the former generally preceding the latter. The rate of leaf maturation is fairly even, however, each successively higher internode elongates and matures at a slower rate than the one next below so that an upper internode may still be elongating while its associated leaf is already fully mature. Differences in the time of maturation of stem tissue and vascular bundles entering the stem from leaves leads to changes in the structural anatomy of the stem from base to apex. Just as races differ in their pattern of growth, the manner and time of structural changes in the stem differ from plants of one race to those of another.

A race such as Argentine pop with a uniform rate of growth shows only slight changes in its structural anatomy from one internode to the next, whereas Zapalote chico with a rapid initial growth rate, which is abruptly slowed down above the position of an ear shoot, has a corresponding sudden change in structural anatomy. Northern flint with a rather even but rapid growth rate undergoes changes similar to those in Zapalote chico but much more gradually. In the upper internodes of such a plant the length of leaves decreases along with the time of stem maturation.

The maize races studied were classified for overall scleroticness on the basis of their hypodermis, peripheral bundle sheaths and sclerified parenchyma and the result was in agreement with field observations on standability. All plants used in the present study were harvested after final maturation and desiccation, at which time it was noted if stems were standing, bent over or broken. Results of this observation are presented below.

Race	No. of plants standing	bent	broken	% plants standing	Strength of stem based on anatomy
Zapalote chico	14	1	0	93%	strong
Papago	13	2	1	87%	strong
Gourdseed	11	4	0	73%	medium strong
Northern flint	10	2	3	66%	medium strong
Chapalote	8	5	2	53%	medium
Argentine pop	3	7	5	20%	weak

The introduction of teosinte germ plasm into maize reportedly leads to an increased induration of all plant parts (Mangelsdorf and Cameron 1942; Galinat et al. 1956). Teosinte plants used in the present study were not especially indurate; in fact, they were less sclerotic than most of the maize races examined. Two plants do not represent teosinte as a whole; nevertheless, they do show that the range of variation within the genus *Euchlaena* includes quite unsclerotic plants. Both species of *Tripsacum* were very sclerotic, but *T. lanceolatum* much more so than *T. dactyloides*. The arrangement of sclerotic tissue in *Tripsacum* is similar to the structure in the upper part of teosinte and most maize races but in lower internodes it is distinctly different from both *Euchlaena* and maize.

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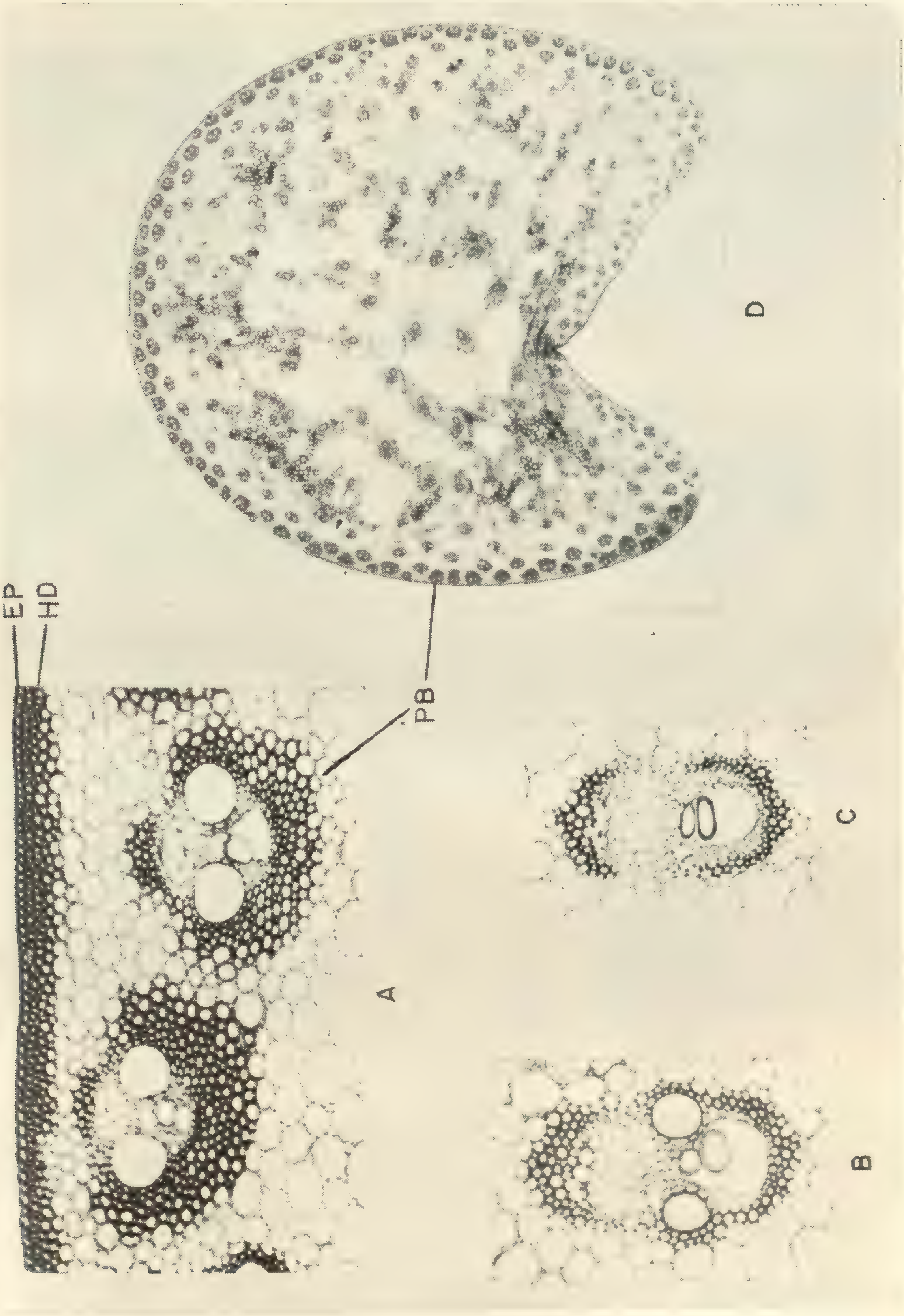
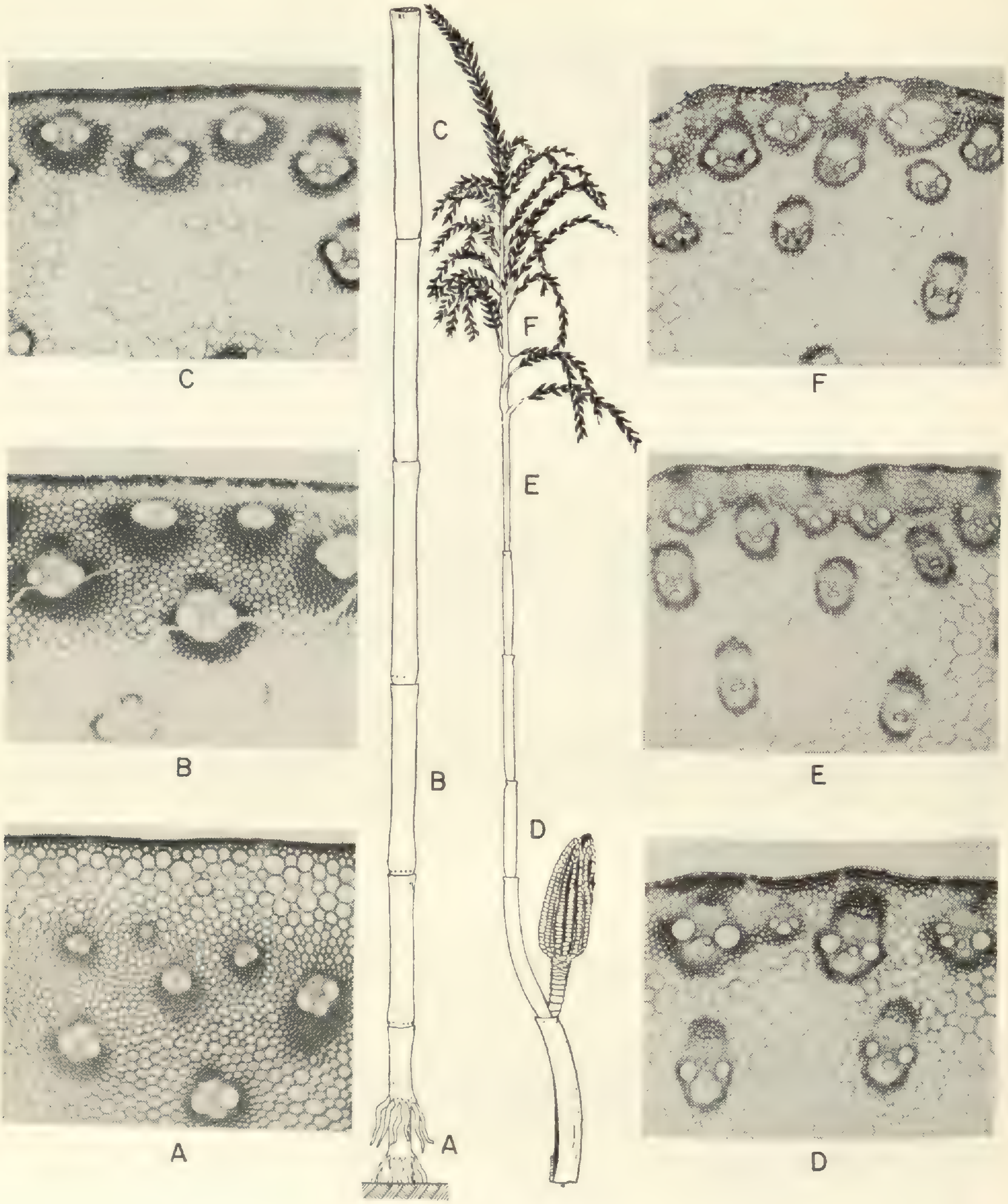
Explanation of Plate

PLATE VI

Structural features of a maize stem. A, Transection of the peripheral region of an internode showing hypodermis (HD), peripheral vascular bundles (PB), and thick-walled parenchyma between the latter (×100). B, Transection of a vascular bundle (×107). C, An atypical vascular bundle lacking well-developed metaxylem vessels. Bundles of this kind were found in the tassel peduncles of all Zapalote plants (×107). D, Transection of a maize stem taken from a middle internode which shows the arrangement of vascular bundles (×7.7).



MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE



MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE

Explanation of Plate

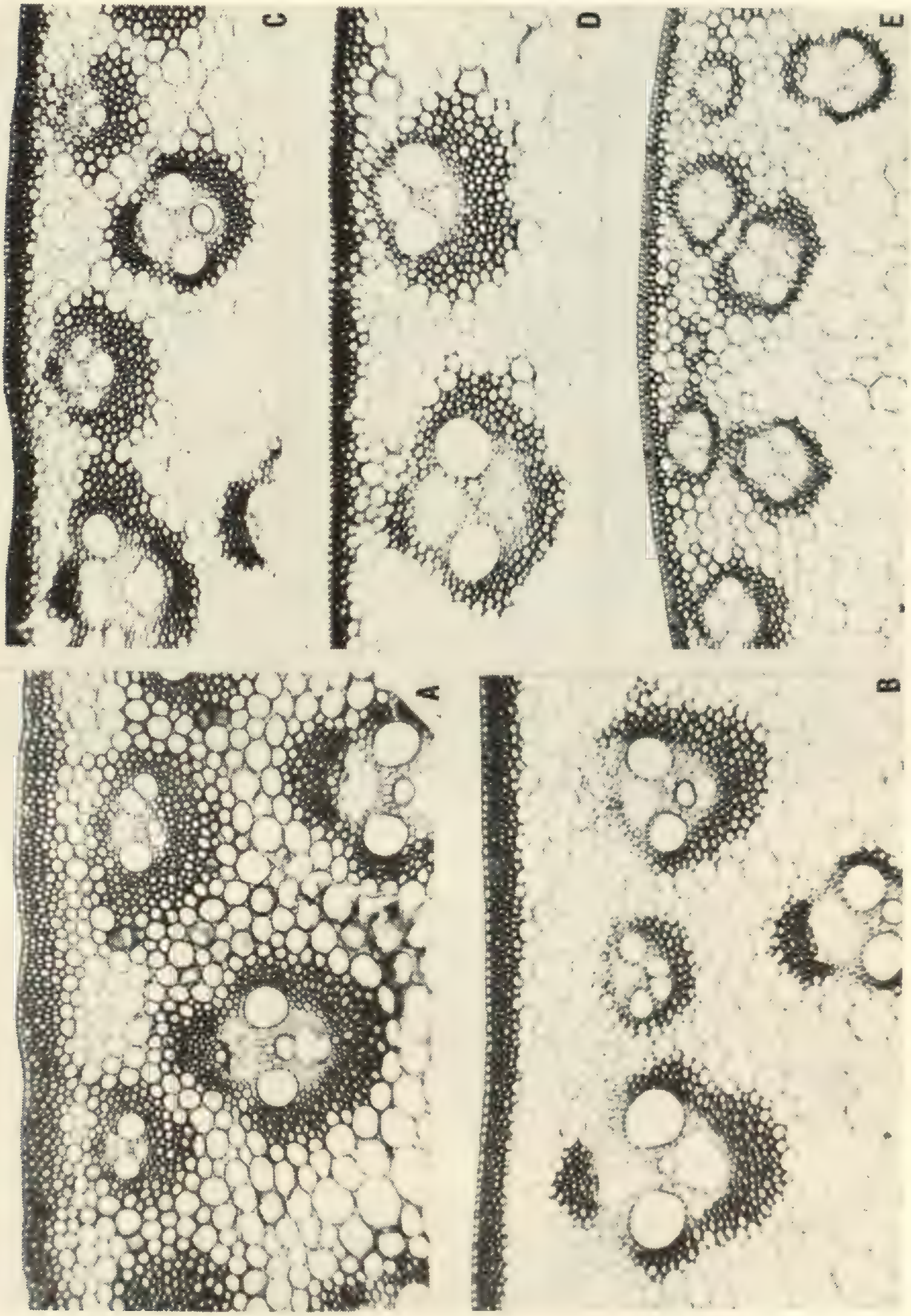
PLATE VII

Scale drawing of a completely mature Zapalote chico plant with leaves removed (1/7 natural size), and transverse anatomical sections from every third internode of this plant to show the changes in structural anatomy occurring in a single stem (×35).

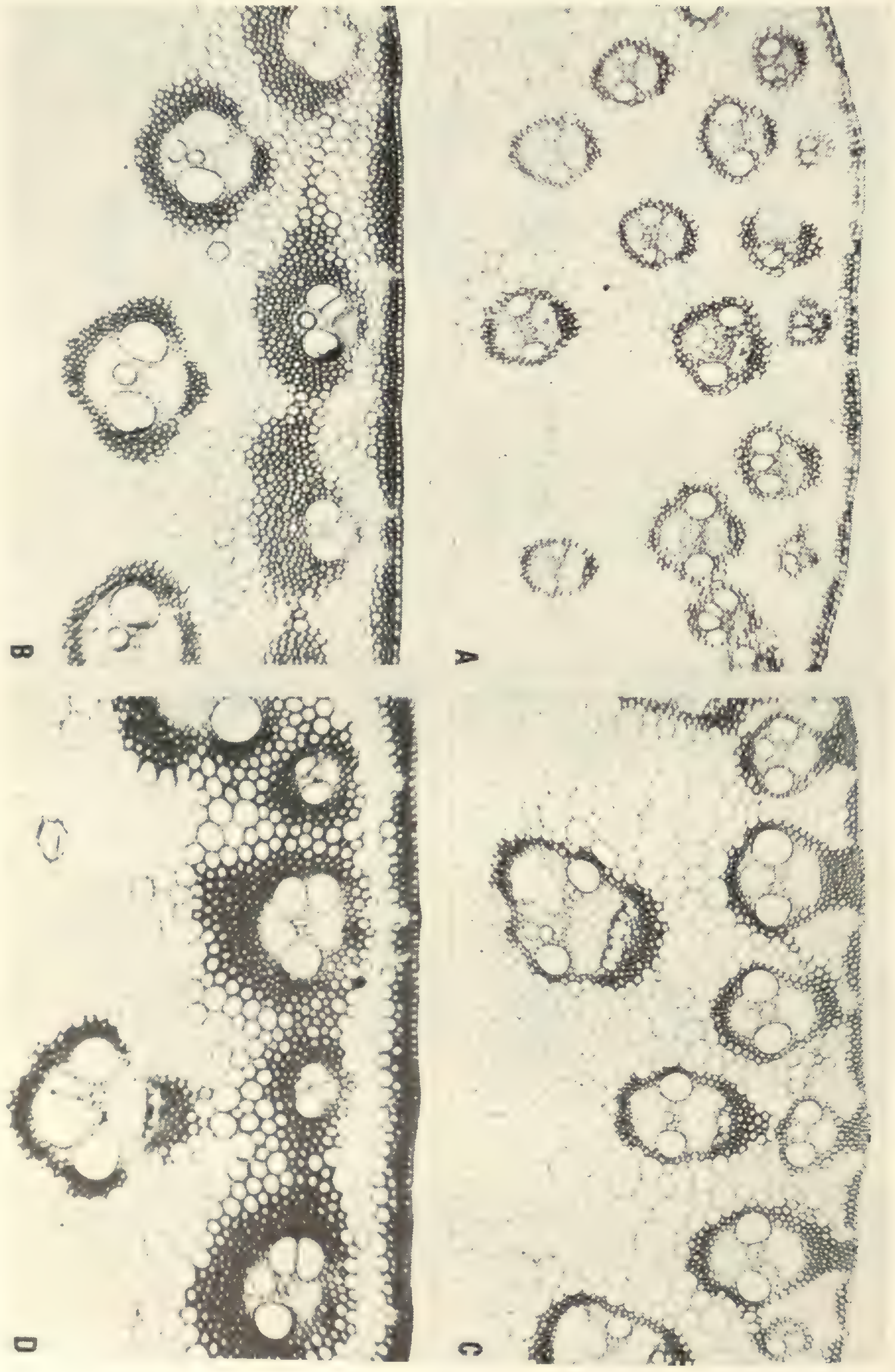
Explanation of Plate

PLATE VIII

Transections of the fourth internode below the tassel peduncle to demonstrate racial differences in hypodermal development (×70). A, Papago; B, Gourdseed; C, Chapalote; D, Northern flint; E, Teosinte.



MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE



MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE

Explanation of Plate

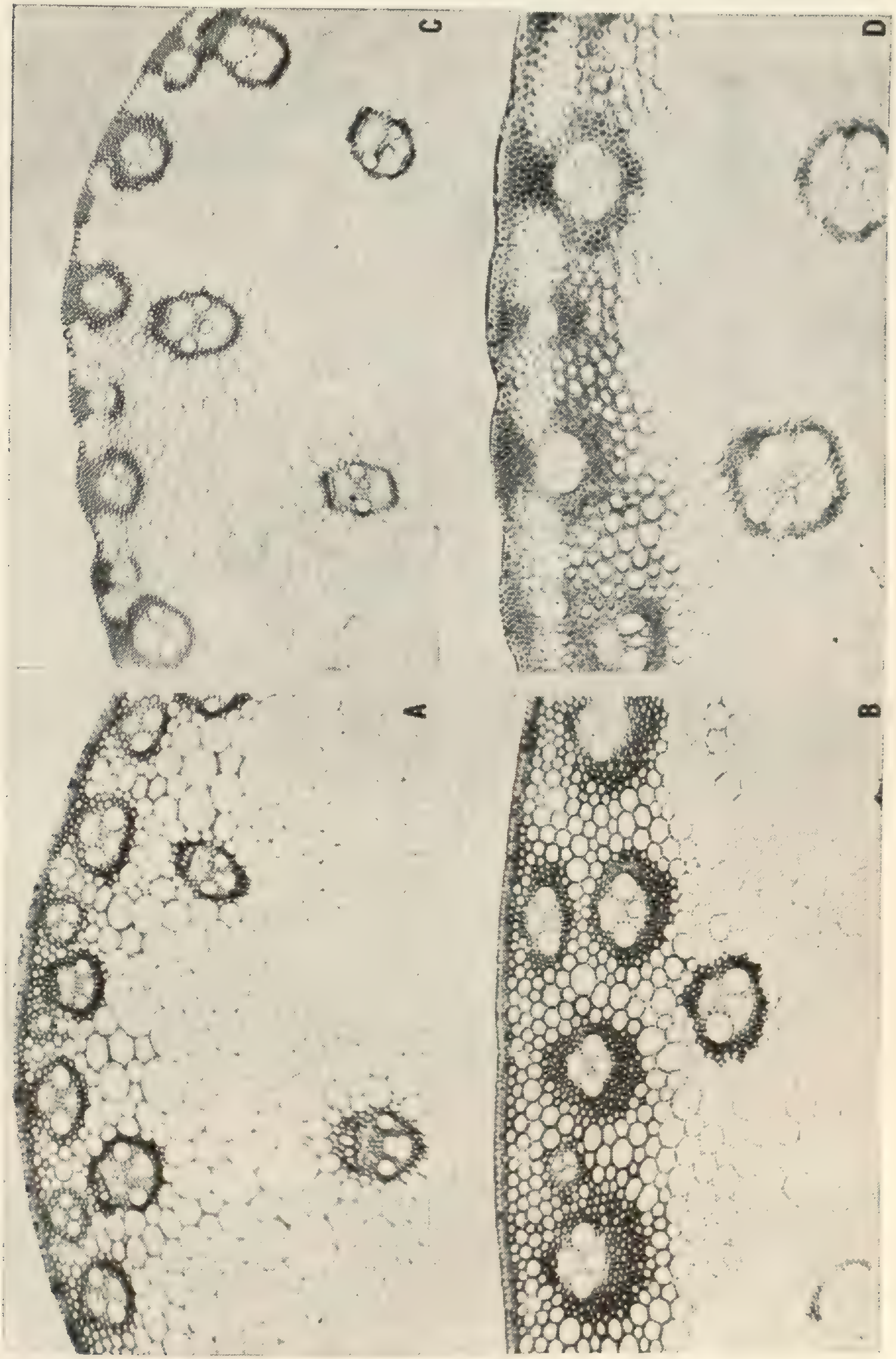
PLATE IX

Internodal transections of Argentine pop (A, B) and Gourdseed (C, D). Upper sections (A, C) made from the tassel peduncle; lower sections (B, D) taken from the eighth internode below the peduncle (×70).

Explanation of Plate

PLATE X

Internodal transections of Teosinte (A, B) and *Tripsacum* (C, D). Upper sections (A, C) made from the tassel peduncle; lower sections (B, D) taken from the eighth internode below the peduncle (×70).



MURDY—STRENGTHENING SYSTEM IN STEM OF MAIZE

STUDIES INVOLVING SUSTAINED TREATMENT OF MAIZE WITH GIBBERELLIC ACID I: FURTHER NOTES ON RESPONSES OF RACES*

NORTON H. NICKERSON AND THOMAS N. EMBLER

ABSTRACT

Field-grown plants of four representatives of three exotic kinds of maize were subjected to four different concentrations of gibberellic acid throughout the growing season. Internode diagrams of controls and treated plants demonstrated that increases in height were taking place in different internodes under different gibberellic acid (GA) concentrations, and that related maizes responded in similar fashion to like GA treatments. General reductions were noted in tiller number, tassel branch number and ear number. High concentrations of GA inhibited growth, eventually killing plants of one race. Degree of inbreeding seems closely associated with GA sensitivity. Male sterility and production of female florets in basal areas of tassels occurred. Brace roots were formed up to 80 cm. above ground. The question of effects of GA on internal mineral balance is discussed briefly. It is suggested that the poor vegetative growth shown by maize plants under excesses of GA may be attributed to a greatly increased rate of respiration. A note of caution is sounded concerning extrapolation to other plant forms of conclusions based on behavior under GA treatment by one cultivar. NORTON H. NICKERSON, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis 10, Missouri; THOMAS N. EMBLER, Dennis-Yarmouth Regional High School, South Yarmouth, Massachusetts.

INTRODUCTION

In previously reported work (Nickerson, 1959), one hybrid, two inbreds and representatives of two exotic kinds of maize were subjected to treatment each third day with four different concentrations of GA. This paper presents results from identical treatment of four other kinds of maize which differ in their behavioral responses.

MATERIALS AND METHODS

Four kinds of maize[1] were employed in this study; they were representatives of three clearly separable races (Anderson and Cutler, 1942). A Northern Flint type (Brown and Anderson, 1947), New York Flint, was chosen to compare its behavior to that of Parker's Flint, a representative employed in the previous study (loc. cit.). Classifiable as "Southern Dent corns" (Brown and Anderson, 1948), Gourdseed (see their Plate 20) and Cherokee Dent (probably a member of their Mexican June complex; see their Plate 22) were chosen both to give a comparison between two forms whose ears were different but whose plant types were not, and to complete the study of Corn-belt ancestral types (Anderson and Brown, 1952a, 1952b) from combinations of which presumably such inbreds as L317 and CC5 investigated earlier (loc. cit.) were derived.

Two ears of Cherokee Dent, one with 12 rows and the other with 14 rows, were obtained from Henry Busby, who in 1959 was about 90 years old. He farms the upper end of an isolated valley near Pollard, Arkansas. His father was a full-blooded Cherokee Indian (or Cherocow, according to his nephew, from whom these details came) who came from North Carolina by way of Tennessee; this strain of maize was brought to Arkansas with him and has been grown, but probably not in complete isolation, by his family since pre-Civil War times. It is the only corn

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[1] Grateful acknowledgement is made to the following individuals for their cooperation in supplying seed: Dr. William H. Murdy, Department of Biology, Emory University, Atlanta 22, Georgia, for Gourdseed; Mr. Derrel Busby, Route 1, Pollard, Arkansas, for Cherokee Dent; Professor A. A. Johnson, Department of Plant Breeding, Cornell University, Ithaca, New York, for New York Flint; Dr. E. G. Anderson, California Institute of Technology, Pasadena, California, for Argentine Pop.

which the family considers fit for human consumption; this fact may have helped keep it relatively uncontaminated. The family refers to this maize as "90-day corn", and often uses it for two crops each year in Arkansas. In New England, at 41° 42′ North Latitude (the equivalent of central Iowa), this maize reached anthesis in 74 days during the 1959 growing season. Fully ripened ears were harvested 35 days later, but it is not known how many days preceding actual harvest date they may have reached ripeness. Its growing season in a cooler more northerly latitude thus approximates 100 days.

A distinctive South American type, Argentine Pop, was also included. This pop corn was collected among others by Cutler in 1941 (personal communication). It has figured prominently in recent genetic work involving the reconstruction of an ancestral maize form (Mangelsdorf, 1958 a, b). According to Alava (1952), Nickerson (1953) and Anderson and Brown (1953), the original source of the strain employed in this study and used for genetical and observational work both at Johnston, Iowa, and Arcadia, California, was seed collected by Mr. Lorenzo Parodi. Plants of both Argentine Pop and Gourdseed have been studied anatomically by Murdy (1960).

In the present study, each type of maize was planted in 15-meter rows; plants were spaced about 25 cm. in the row, and rows were 1½ meters apart. In view of results obtained from randomized rows and blocks of maize in a previous study (Nickerson, 1959) there was no attempt to randomize treatments applied within each row. The total number of plants in each row was divided into five groups with as nearly equal numbers as possible, and all plants in a particular group received the same treatment. The five treatments were the same as those used before and are as follows:

1 — distilled water (controls)
2 — distilled water with 5 ppm GA
3 — distilled water with 25 ppm. GA
4 — distilled water with 125 ppm GA
5 — distilled water with 625 ppm GA

Every third day for the duration of treatments one ml. of the appropriate solution containing either distilled water or water plus the above-listed concentrations of GA[2] was applied from a pipette into the apical leaf cavity of each plant. Solutions were freshly made each time, or stored no longer than three days in darkness at 19° C. Insects (corn borer and corn earworm) were controlled by hand removal and by a weekly dusting of 5% DDT ("Neudust") beginning when evidence of infestation was first noted (July 10) and continuing until elongation ceased and pollination had occurred. Fertilizer (Agrico 5–10–10) was applied at the rate of 700 lbs./acre three and six weeks after germination. Planting date was June 12, 1959; treatments began July 6 and continued until tassel emergence (Table 1).

[2] The GA employed was kindly supplied by Dr. Curt Leben, Agricultural Research Division, Eli Lilly and Company, Greenfield, Indiana.

Results

Initial response in all forms was rapid. Two days after the first treatment had been applied, plants in all treated groups showed increases in height; these ranged up to twice the heights of control plants. During the next two weeks, controls underwent little or no internode elongation; analysis of mature treated plants (Fig. 1) shows that early internode elongation was greatly enhanced by GA, provided that the internode tissue had not reached its final stage of differentiation by the time of treatment. An attempt was made to record the sixth node on each plant by counting all leaves from the coleoptile up (but not the coleoptile itself) when the plants were young. This fifth leaf was known from previous observations to be present on mature plants. It was marked by clipping a metal staple into the leaf. Small arrows on the internode diagrams (Fig. 1) show these sixth nodes as they were determined by fifth-leaf attachment when the plants were mature.

As a precaution against wind damage, many of the rows were staked and plants tied to lines beginning during the fifth and sixth week and continuing throughout the growing season.

New York Flint. (Tables 1, 2, 6; Fig. 1). Higher treatments of 125 and 625 ppm tended to increase lengths of internodes below the ear most drastically; even though upper internode lengths were less than those of the lower internodes in these plants, they were still equal to or greater than upper internode lengths in control plants. Just as noted in the previous study on the closely related Parker's Flint, the 125 ppm treatment proved most detrimental, and there was a recovery toward normal by plants treated with the higher 625 ppm doses. Ear production on plants treated with 125 ppm doses was much lower than with all other treatments. Ears produced by plants treated with 625 ppm doses were much shorter and smaller than those produced by controls, but kernels were set. Tillering was inhibited entirely by treatments of 25, 125 and 625 ppm. The average number of tassel branches was markedly reduced from 15.8 on controls to 6.2 on plants treated with 125 ppm doses. Plants receiving 625 ppm doses produced nearly twice this minimum number, but their average of 11 branches was still only ⅔ the number produced on control plants. Tassels were exserted within 2–3 days in all groups, but anthesis was first noted in plants treated with 25 ppm doses.

Leaves averaged 7 cm. at their widest point on controls. On plants receiving 5 ppm doses, leaves averaged 5 cm. in width and were generally longer by 15 cm. than the same leaves on controls compared just before tassel emergence. Plants treated with 25 ppm doses had at this time leaves as wide as controls but again longer by 15 cm. In plants receiving 125 ppm treatments culm diameter was only half that of control plants; leaves were no longer than control plants, and they averaged only 3 cm. in width at their widest points. The 625 ppm treatments produced plants with quite thin culms (5–10 mm.), long internodes, and compared with controls, much narrower and shorter, occasionally rolled leaves. These rolled leaves were noted previously on plants which were eventually killed by an overdose of GA (Inbreds L317 and CC5; Nickerson, 1959); their rolling may be described

as epinastic with relation to the midrib rather than with relation to the culm, in that the upper epidermis seems to grow more rapidly than the lower to the extent that a tubular structure is formed. A picture of this bizarre feature is shown (for Argentine Pop) in Plate XI. Tassels of these plants all produced female caryopses, but in only two of the four saved for study were these functional. These female spikelets were produced along the basal portions of branches and central spikes.

Brace roots were not formed as copiously on these plants as on Parker's Flint, but primordia did appear as high as 30 cm. above the ground. Their total growth averaged 2–4 cm. Tassel height was significantly increased in plants receiving 5, 25 and 125 ppm doses; it was decreased in plants receiving 625 ppm doses.

Gourdseed. (Tables 1, 3, 6; Fig. 1). All plants treated with GA showed initial responses in height. Plants treated with 5 ppm doses were definitely more vigorous than controls. This vigor was first manifested in increased height; plants 6 weeks old averaged 45–60 cm. compared with an average height of 30–36 cm. for controls. This effect persisted through to maturity. Leaf number (13–14) at 6 weeks was the same for controls, 5 ppm and 25 ppm-treated plants, but with 5 ppm treatments, leaf blades were 10–15 cm. longer than the 75–90 cm. average lengths on controls; leaf blade width at widest point averaged 7–9 cm. compared to the 6–8 cm. average of control plants. The average number of ears and of primary tassel branches showed increases with both 5 ppm and 25 ppm doses compared with controls. Although plants treated with 25 ppm doses reached greater average heights than did those treated with 5 ppm doses, they were not as vigorous as controls. Culms were slightly smaller, and leaves all averaged 6 cm. in width. On plants treated with 125 ppm doses, ear number was not reduced compared to controls, height was not increased over treatments using 25 ppm and primary tassel branch number was reduced only slightly compared to controls. Total tassel height was also about equal to that of controls. Leaves were equal to controls in length, but averaged only 3–5 cm. in width and were easily broken.

Plants treated with 625 ppm doses showed a marked height increase compared to controls; this increase was attributable entirely to greater elongation of lower internodes. Culms however were thinner; leaves averaged only 2–3 cm. wide and were easily broken. Ear number was reduced, tassel height was reduced approximately 14% and the area over which tassel branches arose was greater by 40% when compared to controls. At 11 weeks of age, tassels had fully emerged in all other plants, but not in this group. When they emerged, 3 out of the 5 tassels collected for study had some well-developed caryopses in basal areas of branches and central spikes. In these areas, sessile spikelets were always female and pedicellate spikelets were always male. Of the five tassels, one with caryopses and one with no caryopses were male sterile. Pollen shedding, therefore, was apparently not dependent upon the presence or absence of caryopses in the tassel.

Brace root formation in control and 5 ppm-treated plants was confined to the lower node or two exclusively; in plants treated with 25 ppm doses, they arose on the lower 3–4 nodes. The same number of nodes formed brace roots in plants

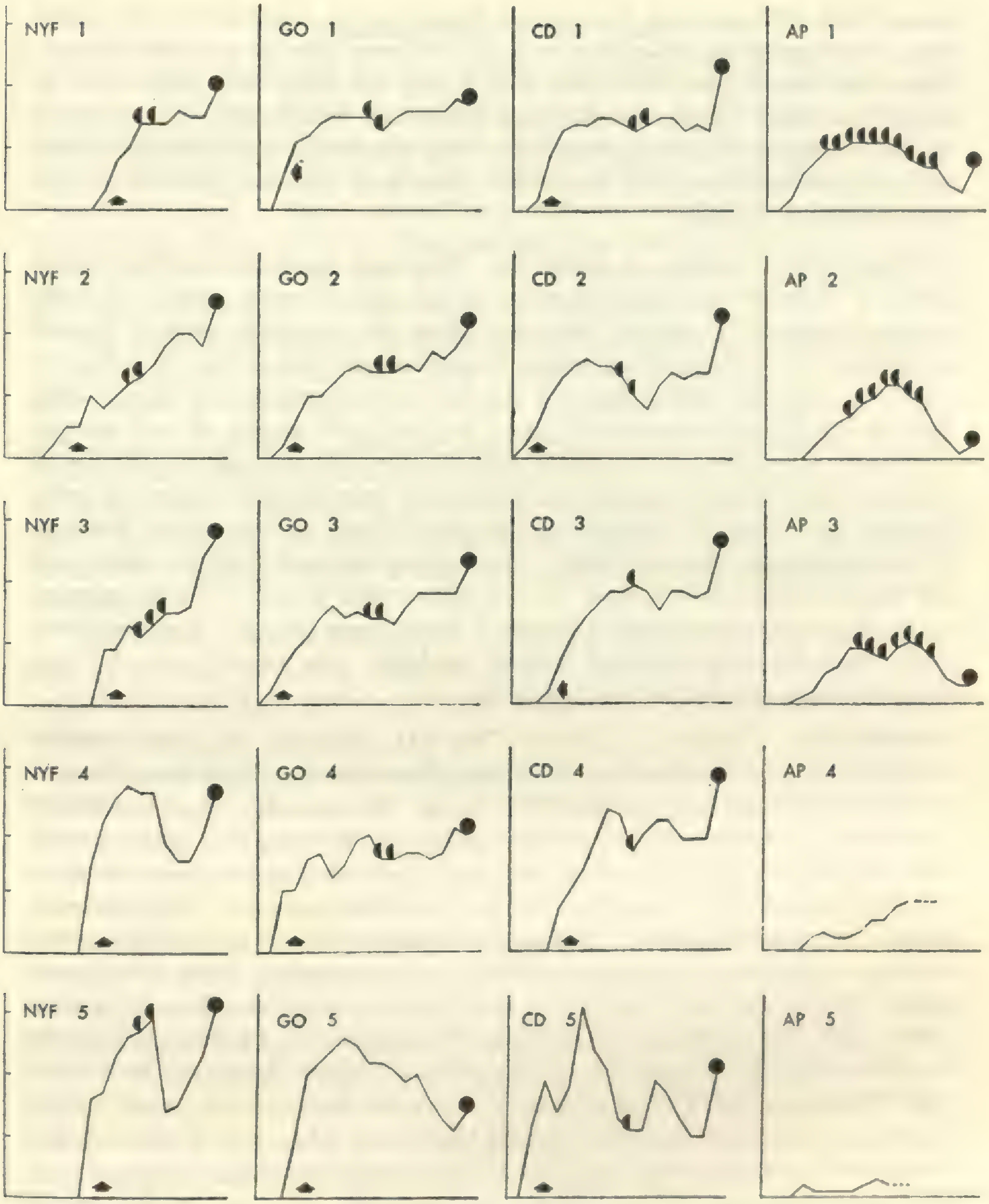

Fig. 1. Internode diagrams of control (top row) and GA-treated maize plants. Horizontal axis is internode number. Vertical axis is internode length; each division is 10 cm. Circle denotes tassel, semicircle denotes ear; arrow depicts node of attachment of fifth leaf above coleoptile.

NYF, New York Flint; GO, Gourdseed; CD, Cherokee Dent; AP, Argentine Pop.

Number 1 stands for distilled water treatments (controls); 2 for 5 ppm GA; 3 for 25 ppm GA; 4 for 125 ppm GA; 5 for 625 ppm GA. Further explanation is given in the text.

treated with 125 ppm, but the extreme lengths of the internodes in this group meant that some of the brace roots were initiated more than 40 cm. above ground. These roots seldom grew more than 3 or 4 cm., and many were only 1 cm. in length. In plants treated with 625 ppm doses, there were consistently five nodes visible on which brace roots had initiated. Root length was also seldom more than 3–4 cm., and for the majority was 1 cm. They were, however, produced as high as 80 cm. above ground.

Cherokee Dent. (Tables 1, 4, 6; Fig. 1). This maize resembled Gourdseed rather closely in responses and appearances of treated and untreated plants. Greatest responses occurred in younger plants; as plant size increased, recovery toward appearance of control plants was noted. Greatest height increase was with doses of 125 ppm; relatively little effect was noted on most measurements except when doses of GA applied contained 625 ppm. At that level, number of ears, number of primary tassel branches, length of central spike and peduncle length showed decreases over the same measurements in controls; only the area over which tassel branches arise showed an increase over controls. Tassels of these plants, however, did not develop any female spikelets. Bending over occurred when the plants were 6–9 weeks of age in the 125 ppm- and 625 ppm-treated groups. The phenomenon occurred in rapidly elongating internodes 1 meter above ground. Such bent-over stalks could not be straightened without breakage. One control plant had the only two tillers observed in this population.

Argentine Pop. (Tables 1, 5, 6; Fig. 1; Plate XI). This race was highly sensitive to all doses of GA. In plants 6 weeks of age, those receiving 5 ppm doses averaged 20–30 cm. in height compared with 15–20 cm. for controls. They had 10–11 leaves visible compared to 8–9 leaves on controls. Tiller number of plants treated with 5 ppm doses was also reduced; at 6 weeks, controls had 2–3 tillers per plant and those treated with 5 ppm doses had only one tiller per plant. This difference was less at maturity, however. Among plants treated with 25 ppm, tiller number and ear number were both reduced below the corresponding values for control plants. A few silks were produced in basal areas of tassel branches and central spikes. Also, leaf width was reduced by half from averages of 5–7 cm. in controls to 2.5–3.5 cm. At 6 weeks, plants treated with 25 ppm doses were 30–37 cm. tall. Plants receiving 125 ppm doses of GA were nearly all eliminated by the treatment; some plants, however, persisted longer than others. At 6 weeks of age, 10 out of 22 plants had been killed; at 11 weeks, only 5 were surviving, and two of these had been mutilated by wind. This mutilation was likely attributable to the extremely brittle nature of these plants. Under doses of 625 ppm, plants showed a strong initial response, but at 6 weeks of age only 8 out of 22 were alive, and at 11 weeks, only one plant was alive. This latter plant was not more than 5 cm. above ground, and its stem was highly contorted (Plate XI). Both doses of 125 and 625 ppm produced plants with thin leaves. In one 125 ppm-treated plant, they were in addition so inrolled that their tips never became free; a "ladder" effect was thus obtained (Plate XI). This plant produced a tassel, never exserted, which was female below and male above; it also lacked tassel branches (Plate XI).

Discussion and Conclusions

This study, along with the previous one (Nickerson, 1959), reinforces the point that the effects of GA on maize are marked, but dependent upon both the race studied and the concentration of GA employed. Internode diagrams (Anderson and Schregardus, 1944) for the four maizes studied were constructed as before, being in each case in Fig. 1 that of an actual plant which best represented its group of five plants studied. These diagrams were constructed from the tassel down, hence the internodes were drawn in the inverse order of their appearance, and tassels are at the same relative position on each graph.

New York Flint and Cherokee Dent show the same pattern of internode elongation above the points of ear attachment. Gourdseed and Cherokee Dent, however, show a much greater similarity with regard to internodal development below the point of ear attachment. Argentine Pop, because of the large number of ears formed, is not comparable to any of the other races. Its growth pattern is here the same as that reported for it by Murdy (1960) under growing conditions in Iowa: the first three internodes are increasingly longer, a plateau is then reached followed by a gradual decline in successive lengths until the longer peduncle is developed.

Vertical comparison of these graphs within each column shows what concentrations of GA affected which internodes within each race of maize: horizontal comparisons show how the various races responded to the same concentrations of GA.

In New York Flint, 5 ppm and 25 ppm treatments produced growth patterns generally alike, affecting most of the internodes above the point of ear insertion. Arrows indicate the point of attachment of the 5th leaf at the top of the fifth internode. The coleoptile is not here counted as the first leaf. Extra internodes were consistently formed below points of ear attachment on plants treated with 125 and 625 ppm GA. An extra internode appears in the diagram of the 5 ppm-treated plant above the point of ear attachment. This observation was true for 4 of the 5 plants measured. Possibly low concentrations of GA applied early enough delay formation of inflorescence primordia for a time. This suggestion is in line with findings of Bradley and Crane (1960) on *Prunus* sp. cultivars, where GA prevented initiation of floral primordia but did not interfere with production of bud-scales.

A comparison between diagrams of New York Flint and Parker's Flint of the previous study (loc. cit.) shows a general similarity of curvature, including the anomalous detrimental behavior under treatments of 125 ppm. The fact that New York Flint plants treated with 5 and 25 ppm doses exhibit less departure from the control growth pattern than do plants of Parker's Flint treated with these same doses may be interpreted as signifying that New York Flint has in its genetic makeup some other maize germ plasm and is not therefore as "pure" a representative of Northern Flint as is Parker's Flint.

Gourdseed shows remarkably little internodal pattern change under doses of 5,

25 and 125 ppm compared with controls; under treatments of 625 ppm, its curve is quite similar to that for 125 ppm-treated New York Flint. These results may likewise be interpreted as indicating that Gourdseed is in itself not a "pure" representative of its race, Southern Dent; its hybrid ancestry, referred to by Brown and Anderson (1948), has apparently buffered its protoplasmic reactions to GA. This same situation may be seen in the previous experiments (loc. cit.) with regard to Spancross, a known hybrid. In fact, in its general slight effect on 5, 25 and 125 ppm-treated plants, and its stimulation of early internodes followed by declines in length except for the peduncle, GA creates much the same effect on both Gourdseed and Spancross. The general beneficial effect of low doses of GA on Gourdseed have been alluded to above; it is possible that GA may find commercial importance in boosting yields on maize strains which are strongly of Southern Dent ancestry.

Gourdseed also has much in common with the internode pattern of Zapalote Chico, a race also previously studied (loc. cit.). The two maizes respond nearly alike to treatments with 5 ppm and 25 ppm doses; with the higher concentration of 125 ppm, Zapalote Chico shows more sensitivity to GA than does Gourdseed. When the GA concentration was highest (625 ppm) their developmental patterns were again strongly similar.

Cherokee Dent, based on its lower row number and less conspicuous denting, is also a representative with mixed genetic background. This contention is borne out by relatively slight differences in internode patterns of controls, 5, 25 and 125 ppm treatments. There are also strong resemblances between its responses and those of both Gourdseed (see above) and Zapalote Chico of the previous study (loc. cit.). Brown and Anderson (1948) mentioned that the Southern Dents were a variable lot and that on both cytological and morphological evidence they showed a strong affinity to the dent corns of central Mexico. This contention was accepted fully by Wellhausen et al. (1952). In their general internode patterns of control plants and in their similar responses to various doses of GA, these resemblances are further confirmed.

Argentine Pop, as it is grown in the United States, is known to be a highly inbred race. Two sorts, based on plant height and ear size, were segregated out of the original collections independently in studies conducted at Johnston, Iowa, (Edgar Anderson, personal communication) and at Arcadia, California, (E. G. Anderson, personal communication). Cutler (personal communication), who has collected and observed Argentine Pop in its native range in South America, regards it as being essentially inbred there also. He also reported the taller, fewer-eared segregants as not being "uncommon". This race may therefore be considered to be a rather pure one. The present study, however, used material which for several generations has always produced small ears in large numbers. Ears of this distinctive race have been figured by Weatherwax (1954, fig. 59) and Mangelsdorf (1958 a, b; fig. 6).

In its strong sensitivity to GA, Argentine Pop resembles responses of the inbreds

CC5 and L317 studied previously (loc. cit.). Higher doses are fatal; in Fig. 1, the only survivors of the 125 ppm and 625 ppm groups are graphed simply to show the extent to which deleterious reactions may go and still allow the plant to remain alive. These two plants were collected and later photographed (plate XI). The well-documented effects of GA on reduction of tiller number and ear number were also graphically illustrated (table 5). Tassels of 25 ppm-treated plants developed a few silks and female spikelets; the one non-exserted tassel of the 125 ppm-treated survivor showed a completely female basal portion and a male but sterile tip portion (Plate XI). Its general resemblance to a basal immature inflorescence is remarkable.

It may therefore be concluded that GA affects maize in a fashion depending directly upon the degree of inbreeding or homozygosity of the strain involved. Since there are now many forms of maize, and since they exhibit a vast range of human control or lack of it over their past pollinations, it seems reasonable to conclude that responses of no one form of maize are "standard".

It is precisely because of such racial or varietal differences that generalized conclusions, especially where a variable cultivated plant is used as experimental material, must be based upon wide studies. As an example one might compare the explanation offered for the predominant way in which GA acts in plant elongation by Feucht and Watson (1958) with that of Greulach and Haesloop (1958). The former workers, using the cultivar Blue Lake of *Phaseolus vulgaris*, concluded that cell elongation was primarily responsible for GA-induced increase in internode length. The latter workers, using the cultivar Black Valentine of *Phaseolus vulgaris*, concluded that only cell division was responsible for GA-induced increase in internode length. Paleg and Aspinall (1958) reported differences in response to GA under the same environmental conditions in two varieties of barley. Kline (1959), working with celery plants, showed that age of plant was also important in eliciting a particular response. He suggested it may be more important even than dosage of GA applied. Other examples might also be cited; these instances referred to above, however, reinforce the argument for caution in extrapolative interpretation of results.

The rather marked increase in length of peduncles in most treated groups (Fig. 1; Table 6) as well as a general increase in height of tassels (Table 6) are likely attributable directly to the influence of GA on these parts when the plant is quite young. Murdy (1960) has pointed out, as has Kiesselbach (1949), that the peduncle and tassel of maize mature relatively early at a time when internodes below are still immature.

The thin culms and general lack of vigor in maize plants treated with high doses of GA may be a direct result of higher-than-normal respiratory rates. Using wheat seedlings, a 20% rise in respiration under treatment with GA has been reported by Luštinec and Krekule (1959). Coulombe and Paquin (1959), working with tomato, reported rapid increase in respiration, photosynthesis and transpiration with a peak 5–6 hours after treatment, followed by a rapid decline, but higher respiration and photosynthesis rates than controls during limits of their experiment. Ormrod and Williams (1960) found that plants of *Trifolium hirtum*

showed a striking increase in acid soluble phosphorus and decrease in inorganic phosphorus as quickly as one minute after treatment with GA. Using bean plants, Linck and Sudia (1960) showed that GA-treated plants absorbed more P^{32} than did controls. There thus may be a correlation between GA treatment, respiratory rate and phosphorus metabolism.

The phenomenon of poor leaf separation, noted occasionally in all forms given higher treatments with GA in both this study and the previous one and illustrated by Plate XI, resembles illustrated symptoms of calcium deficiency (Hambidge, 1941). Went (1957) similarly noted this same "harp-like" structure on corn plants grown under continuous light.

The brittleness of maize plants treated with higher concentrations of GA may be because of mineral imbalance within the plant. In carnations, Laurie and Kiplinger (1948) reported that overdoses of potassium will cause brittleness and snapping off at nodes. Whether the GA-induced aberrations in mineral content of maize plants also causes a potassium imbalance resulting in brittle stems and leaves is not known. It may only be concluded that overdoses of GA apparently upset mineral balances in plants.

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TABLE 1

TOTAL AMOUNT OF GA RECEIVED BY EACH PLANT IN MICROGRAMS

	No. of Treatments	Amount of GA per treatment 0	5	25	125	625
New York 8-rowed Flint	15	0	75	375	1875	9375
Gourdseed	18	0	90	450	2250	11250
Cherokee Dent	15	0	75	375	1875	9375
Argentine Pop	19	0	95	475	2375	11875

TABLE 2—NEW YORK FLINT

	Treatment in ppm of GA	0	5	25	125	625
Averages of 5 plants in each treatment group	Height (nearest cm.)	126	164	170	233	204
	Number of Nodes	10	12	11	11.25	10.75
	Number of Tillers	2.6	2.6	0	0	0
	Number of Ears	2.0	2.0	2.2	0.25	0.75
	Number of Primary Tassel Branches	15.8	11.8	12.6	6.2	11
	Percent of Tassels Wholly Male Sterile	0	0	0	100	100
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	25	75
	Original Size of Population	17	17	17	18	18
	Number Surviving	16	16	17	13	11
	Number of wind-damaged plants among survivors	0	0	0	3	7

TABLE 3 — GOURDSEED

	Treatment in ppm of GA	0	5	25	125	625
Averages of 5 plants in each treatment group	Height (nearest cm.)	211	220	243	243	262
	Number of Nodes	15.2	15.4	16.8	15.6	15.6
	Number of Tillers	0	0	0	0	0
	Number of Ears	1.4	2.2	1.6	1.4	0.8
	Number of Primary Tassel Branches	12.4	14.6	13.0	11.8	11.8
	Percent of Tassels Wholly Male Sterile	0	0	0	0	40
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	0	60
Original Size of Population		25	21	23	23	24
Number Surviving		25	20	23	22	24
Number of wind-damaged plants among survivors		0	0	0	10	12

TABLE 4 — CHEROKEE DENT

	Treatment in ppm of GA	0	5	25	125	625 (3 plants)
Averages of 5 plants in each treatment group	Height (nearest cm.)	218	233	235	275	255
	Number of Nodes	15.8	16.6	15.8	15.2	16.4
	Number of Tillers	0.2	0	0	0	0
	Number of Ears	2.2	2.2	1.8	2.0	0.6
	Number of Primary Tassel Branches	21.8	25.6	23	18.8	16
	Percent of Tassels Wholly Male Sterile	0	0	0	0	30%
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	0	100%
Original Size of Population		17	18	18	18	17
Number Surviving		14	17	18	17	13
Number of wind-damaged plants among survivors		0	0	3	7	10

TABLE 5 — ARGENTINE POP

	Treatment in ppm of GA	0	5	25	125	625
Averages of 5 plants in each treatment group	Height (nearest cm.)	101	87	83 (3 plants)	46	Insuff. No. of Plants
	Number of Nodes	14.2	13.4	15.2	13.0	Insuff. No. of Plants
	Number of Tillers	4.2	3.0	1.2	0	Insuff. No. of Plants
	Number of Ears	7.6	7.6	5.8	0	Insuff. No. of Plants
	Number of Primary Tassel Branches	22.4	21.6	20.8	No tassels exserted	
	Percent of Tassels Wholly Male Sterile	0	0	0	No tassels exserted	
	Percent of Tassels with some Functional Pistillate Florets	0	0	0	No tassels exserted	
Original Size of Population in Each Treatment Group		23	22	22	22	22
Number Surviving		23	17	14	5	1
Number of wind-damaged plants among survivors		0	0	3	2	0
Number of plants dying from treatment		0	5	8	17	21

TABLE 6
5-PLANT-AVERAGE LENGTHS OF CERTAIN MEASUREMENTS CONTRIBUTING TO HEIGHT

Treatment of GA in ppm.		0	5	25	125	625
Central spike length (cm.)	New York Flint	24.0	31.8	27.5(4)*	31.0(2)	10.0(4)
	Gourdseed	24.0	23.6	24.8	21.2	18.6
	Cherokee Dent	26.6(3)	23.0	28.2(4)	24.0(4)	19.6(3)
	Argentine Pop	17.8	19.0(4)	19.4	—	—
Branching area below central spike (cm.)	New York Flint	11.4	10.2	15.2	14.8(4)	13.2(4)
	Gourdseed	10.4	12.4	12.8	14.0	11.8
	Cherokee Dent	15.6	17.4	16.8	16.2	18.3(3)
	Argentine Pop	9.0	8.6	7.8	—	—
Peduncle length (cm.)	New York Flint	17.2	24.2	28.2	25.8(4)	21.8(4)
	Gourdseed	19.0	19.0	17.4	18.6	11.8
	Cherokee Dent	23.0	21.0	24.6	22.4	14.0(3)
	Argentine Pop	5.0	2.8	2.8	—	—
Tassel height (branching area plus central spike of tassels in cm.)	New York Flint	35.4	42.0	42.7	45.8(4)	23.2
	Gourdseed	34.4	36.0	37.6	35.2	30.4
	Cherokee Dent	42.2	40.4	45.0	40.2	37.9(3)
	Argentine Pop	26.0	27.6	27.2	—	—

* Numbers in parentheses refer to number of plants from which measurements were made when 5 plants were not available.

Explanation of Plate

PLATE XI

Argentine Pop. Plant on right treated with 125 ppm GA each three days for entire growing season. Note ladder-like effect of leaves joined at tips. Bulge at top containing small ear photographed at extreme left; top photo is dry ear, while lower photo is same ear gently boiled in water and partly dissected. Note male spikelets at top, paired female spikelets (2 silks at base of lower left-hand photograph indicate one pair) and lack of tassel branches. Well-developed cupules are also found on this tassel; line marked *C* indicates one in oblique view. Plant in center is contorted culm and leaves of only surviving maize plant in group receiving 625 ppm GA. Brace roots were thin, brittle and poorly developed on both plants. Black and white checked ruler divisions are 1 cm. each; fine divisions are 1 mm. each.

NICKERSON & EMBLER—GIBBERELLIC ACID TREATMENT I

STUDIES INVOLVING SUSTAINED TREATMENT OF MAIZE WITH GIBBERELLIC ACID II: RESPONSES OF PLANTS CARRYING CERTAIN TASSEL-MODIFYING GENES*

NORTON H. NICKERSON

ABSTRACT

Plants containing each one of seven different tassel-modifying genes were treated with Gibberellic Acid–distilled water mixtures every three days throughout the growing season until tassel emergence. GA was found to suppress expression of ramosa-1 (ra_1). Tassel-seeds 2 (ts_2), 5 (Ts_5) and 6 (Ts_6), Tunicate (*Tu*) and Vestigial glume (*Vg*) were all modified, but not so much that they could not be recognized. The recessive male-sterile 1 (ms_1) remained male-sterile. An explanation of certain elongation patterns in these plants is tentatively made, which points toward the idea that GA depends at least in part on the presence of auxin (IAA) for its effects. NORTON H. NICKERSON, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

INTRODUCTION

Phinney (1956) showed that *dwarf-1*, a recessive maize mutant, responded to Gibberellic Acid (hereinafter called GA) in such a way as to become phenotypically normal with a total amount of 60 micrograms of GA applied regularly during the growing season. Recently (Nickerson, 1960a) it has been shown that the dominant maize genes Corn-grass (*Cg*) and Teopod (*Tp*) likewise respond to sustained GA treatments in a like manner, becoming essentially normal in phenotype. It has also been shown previously (Nickerson, 1959; Nickerson and Embler, 1960) that normal maize plants respond to sustained treatment with GA in several characteristic ways. Inasmuch as some of the growth manifestations noted under such GA treatment resembled some known tassel mutants, it was decided to grow obtainable seed of a series of tassel mutants previously studied (Nickerson and Dale, 1955) and subject them to various strengths of GA treatment throughout their growing seasons. The maize mutants[1] Tassel-seed 2 (ts_2), Tassel-seed 5 (Ts_5), Tassel-seed 6 (Ts_6), Vestigial glume (*Vg*), Tunicate (*Tu*), Ramosa-1 (ra_1) and Male-sterile 1 (ms_1, later shown to be identical to tassel-seed 8 of Nickerson & Dale, 1955) were grown, treated and studied.

MATERIALS AND METHODS

Planting distances and cultural methods employed are the same as those set forth in an earlier account (Nickerson and Embler, 1960). There were generally 2 or 3 lots of seed available for each of the above-listed mutants. Each of the stands of plants resulting from these seed lots was divided into four groups with as nearly equal numbers as possible; all plants in a particular group received the same treatment.

Concentrations of GA chosen were in the range shown by a previous study (Nickerson, 1959) to have a detectable but not drastic effect on field-grown maize plants. The four treatments employed were as follows:

1 — distilled water (controls)
2 — distilled water with 50 ppm GA

* This work was supported by a grant from the National Science Foundation.

[1] Thanks are hereby gratefully extended to Dr. Earl B. Patterson, Department of Botany, University of Illinois, Urbana, Illinois, for providing seed from Maize Genetics Cooperation sources for this study.

3 — distilled water with 100 ppm GA
4 — distilled water with 150 ppm GA

Each third day for the duration of treatments one ml. of the appropriate solution containing either distilled water or water plus the above-listed amounts of GA[2] was applied from a pipette into the apical cavity of each plant. Solutions were freshly made each time, or stored no longer than three days in darkness at 19° C. Planting dates, beginning treatment dates, ending treatment dates, total numbers of plants grown and total amounts of GA applied to each mutant are shown in Table I.

Results

Tassel-seed 2 (ts_2). Seed stocks employed had no normal sibs. Because of the extreme general uniformity of plants within each treatment group, measurements were made only on four single treated plants exhibiting the mutant form (Table II). Central spike length was generally decreased with increasing dosage, as were the number of primary tassel branches, the area over which they originated, and the number of ears produced. Peduncle length was about equally decreased by all three dosage levels of GA. Internode number was hardly influenced at all. Plant height showed increase with GA treatment; each group of treated plants in the field was highly uniform in total plant height, but internode diagrams (Fig. 1) show that early-formed internodes were increasingly lengthened by increasing doses of GA, while later-formed ones became much shorter than those of the distilled-water-treated mutant plant. Specimen tassels show a rapid decrease in overall size, but proportions of peduncle length, branch number, spikelet number and caryopsis development remain relatively constant (Plate XII).

Tassel-seed 5 (Ts_5). Plants were either normal (+/+) or heterozygous (Ts_5/+) in genetic constitution. Figures listed under "M" on Table II are averages for 4 mutant (Ts_5/+) plants; figures listed under "C" are measurements for the single control (+/+) plant in that group. Length of central spike was depressed solely by doses of 100 ppm GA in mutant-carrying plants; only slight changes were manifested in normal sibs. Tassel branch numbers fluctuated with no definite pattern in treated mutant-carrying plants; a consistent reduction was noted by all strengths of GA employed on normal sibs. The length of stem over which tassel branches developed was relatively consistent for both mutant-carrying and normal sibs regardless of GA concentration employed. Peduncle length of normal sibs was relatively uniform, but 50 ppm doses of GA tended to shorten this length somewhat in mutant-carrying plants, while 150 ppm doses tended to lengthen peduncles by about the same amount. Internode number increases consistently in mutant-carrying plants with increasing dosage; in normal sibs the number is uniformly increased by all GA levels employed. Ear number is increased in both mutant-carrying plants and normal sibs by doses of 50 ppm GA; further increase in GA dosage level does not decrease ear number in mutant-carrying plants, but drastically does so in normal sibs.

Plant heights of mutant-carrying plants, nearly equal to those of normal sibs

[2] The GA employed was kindly supplied by Dr. Curt Leben, Agricultural Research Division, Eli Lilly and Company, Greenfield, Indiana.

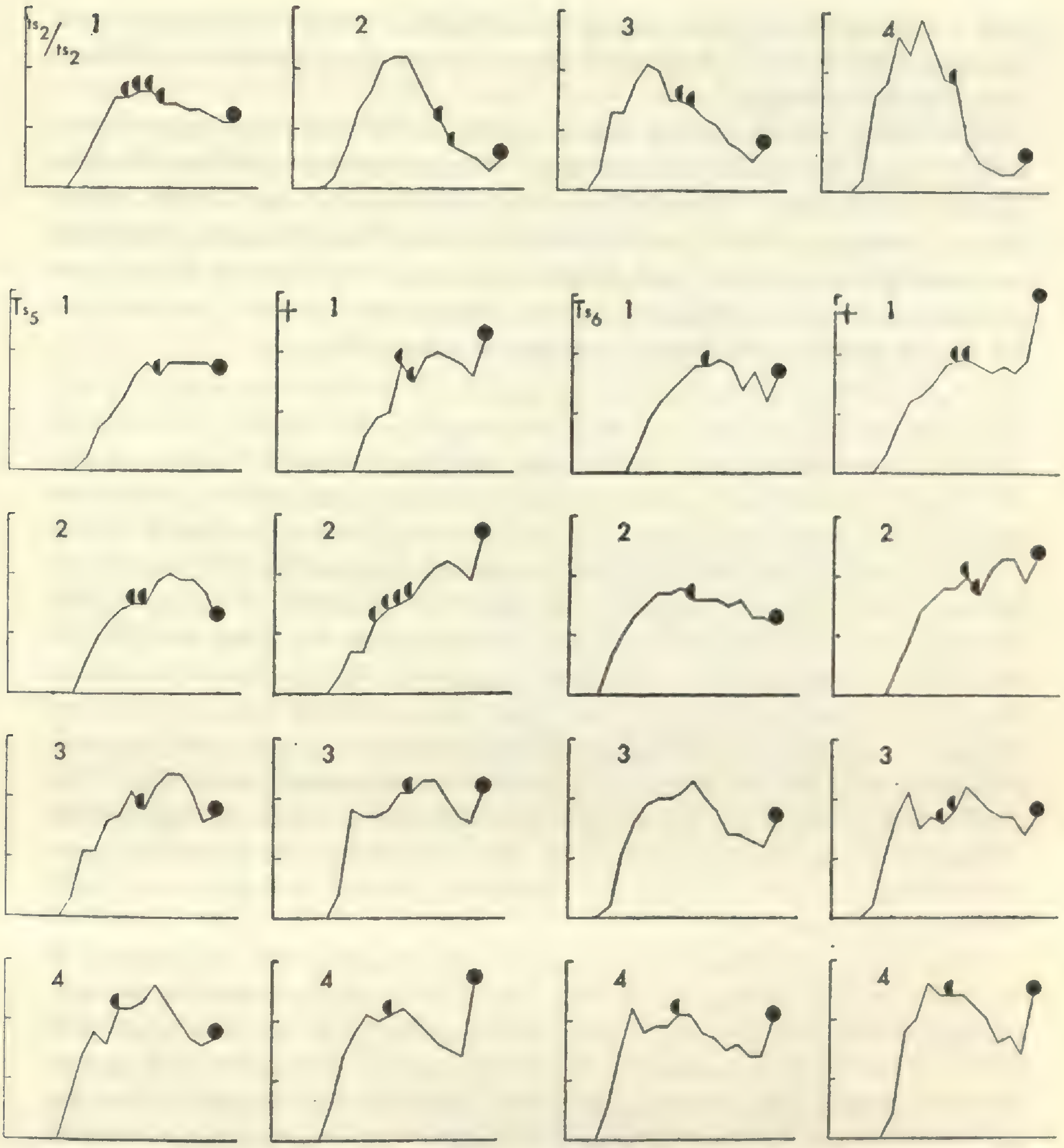

Fig. 1.

Figs. 1–3. Internode diagrams of various maize plants with either normal or mutant conditions showing responses to treatment with GA. Numbers are indicative of treatments, as follows: 1, distilled water; 2, 50 ppm GA; 3, 100 ppm GA; 4, 150 ppm GA. Internode lengths are indicated in 10-cm. units on ordinate; internode number may be determined from the abscissa. These graphs were all plotted from the tassel down, so all tassels (dots) are in the same relative position on each graph. Ears are represented as semicircles.

under control (H_2O) doses, are not as sensitive as those of normal sibs until the GA dosage reaches 150 ppm. Analysis of internode diagrams show that peduncle lengths in normal sibs are as long or longer than the longest lower internodes. The consistent dip below the peduncle and above the ear is present in all cases. With increase in dosage, early-formed internodes become longer. Mutant-carrying plants

show a different form from normals under control (H_2O) treatments; with increasing doses of GA, it is the internodes above the ear and below the peduncle which become the longest.

Plate XIII, No. 1 shows both control plants (left of ruler) and plants treated with 150 ppm GA doses (right of ruler). Normal sibs are above and mutant-carrying sibs are below. Increased peduncle lengths may be seen on both treated plants. Reduction in tassel branch number in normal sibs is prominent; branches on treated plants are also more loosely organized. More female florets were developed on GA-treated mutant-carrying sibs than on untreated controls, but GA did not stimulate formation of caryopses in normal sibs.

Tassel-seed 6 (Ts_6). Plants were either normal (+/+) or heterozygous (Ts_6/+) in genetic constitution. As with the foregoing, "M" in Table II refers to averages of measurements made on 4 mutant individuals while "C" refers to values for a single normal plant under the same treatment condition. Central spike length was not greatly decreased by any GA treatments in either mutant or normal forms. Tassel branches, however, were consistently increased in the mutant with increasing GA concentration and at the same time decreased in normal plants. Branching area was increased in mutants with increased GA doses, but did not vary greatly in normal plants. Peduncle lengths were greatly modified by lower doses of GA, but the high level (150 ppm) approached the average of control mutants. In normals, the 100 ppm dosage produced the most noticeable depression in length, a fact also consistent with the behavior of normal sibs of Ts_5. Ear number was in general reduced by treatment with GA, but only the highest dose (150 ppm) affected the normal sib in this way. More internodes on mutant plants seem to have elongated with GA than without it, but no consistent trend could be noticed in normal sibs.

Plant heights of mutants were increased with increasing GA dosage; doses of 150 ppm increased total height by 50%. By contrast, normal sibs with the same dosage increased only by 11%. Internode diagrams (Fig. 1) show that with distilled water, lower internodes are about the same in length and general gradual increase in both mutant-carrying and normal sibs; it is the internodes above the ear which account for their differences in height. 50 ppm treatments seem to stimulate all internodes about equally, except for a reduction in peduncle length of the normal sib. 100 ppm of GA has a greater stimulation of lower internodes but apparently tends to shorten all upper internodes. 150 ppm doses on both mutant-carrying and normal sibs show a marked effect on the early internodes with a peak length reached below the ear; each internode is then shorter up until the peduncle, which although long, does not exceed the longer internode. A comparison between these last curves shows a considerable amount of similarity.

Plate XIII, No. 2 shows tassels from mutant-carrying and normal sibs. Those on the left of the ruler received treatment with distilled water; those on the right with 150 ppm GA. Peduncle growth in mutant-carrying plants is notable, reduc-

tion of silks and increase in stiffness of branches are likewise easily seen. Some female florets are developed at the base of the normal sib's branches and central spike; its reduced branch number can also be seen. No developed kernels have been found in any of the 15 control mutant-carrying tassels studied. In those treated with 150 ppm GA, several normal-sized caryopses were noted in three out of four tassels. These caryopses always were in the same basal locations at which caryopses develop in normal sibs under this same treatment.

Vestigial glume (Vg). Plants were either normal (+/+) or heterozygous (Vg/+). In Table III, "M" refers to average measurements of 4 mutant-carrying plants and "C" to measurements of single normal sibs. Central spike length was reduced but not consistently by GA in both mutant-carrying and normal sibs. Tassel branch number was increased by 50 ppm doses on mutant-carrying plants and decreased by both 100 and 150 ppm doses. On normal sibs, tassel branch number was reduced consistently by all GA doses. Tassel branching area for both mutant-carrying and normal sibs showed little or no response to GA. Peduncle length was reduced by 50 and 150 ppm GA treatments in mutant sibs; in normals, both 50 and 100 ppm GA treatments caused reductions, but 150 ppm doses resulted in a peduncle length close to that of the distilled water-treated plant.

Ear number was generally increased on mutant-carrying plants with increased GA concentration; ear number on normal sibs was increased by doses of 100 ppm GA, but doses of 150 ppm GA completely inhibited ear formation. Numbers of elongated internodes were increased by GA in mutant-carrying sibs by all concentrations of GA; approximately the same results were noted in normal sibs.

Plant heights were adversely affected in both groups by 50 ppm GA doses; in normal sibs, 100 ppm doses produced even shorter plants, while 150 ppm doses produced the tallest plants. In mutant-carrying sibs, an adverse effect is also noted by 50 ppm GA doses, but 100 ppm doses produced a greater average height than doses of 150 ppm. Internode diagrams (Fig. 2) show similar curves for both mutant-carrying and normal sibs. Doses of 50 ppm GA markedly depress elongation of internodes above the ears and do not influence internode length below the ears. With doses of 100 ppm GA early-formed internodes are greatly elongated and later-formed ones even more drastically reduced. Curves for plants which have been subjected to doses of 150 ppm GA show that internodes immediately below sites of ear formation are most greatly stimulated in elongation while those immediately below the peduncles are most strongly inhibited in elongation.

Plate XIV, #1 is of normal sibs (upper tassels) and mutant-carrying sibs (lower tassels) of plants treated with distilled water (left of ruler) and 150 ppm doses of GA (right of ruler). Tassel branch reduction under GA treatment is apparent. Shortening of the mutant-carrying peduncle by GA may also be seen. Production of female caryopses (florets) does not occur in either normal sibs or mutant-carrying plants with this dosage; a very few are developed at the base of the lowermost tassel branch under 100 ppm doses in both mutant-carrying and normal sibs.

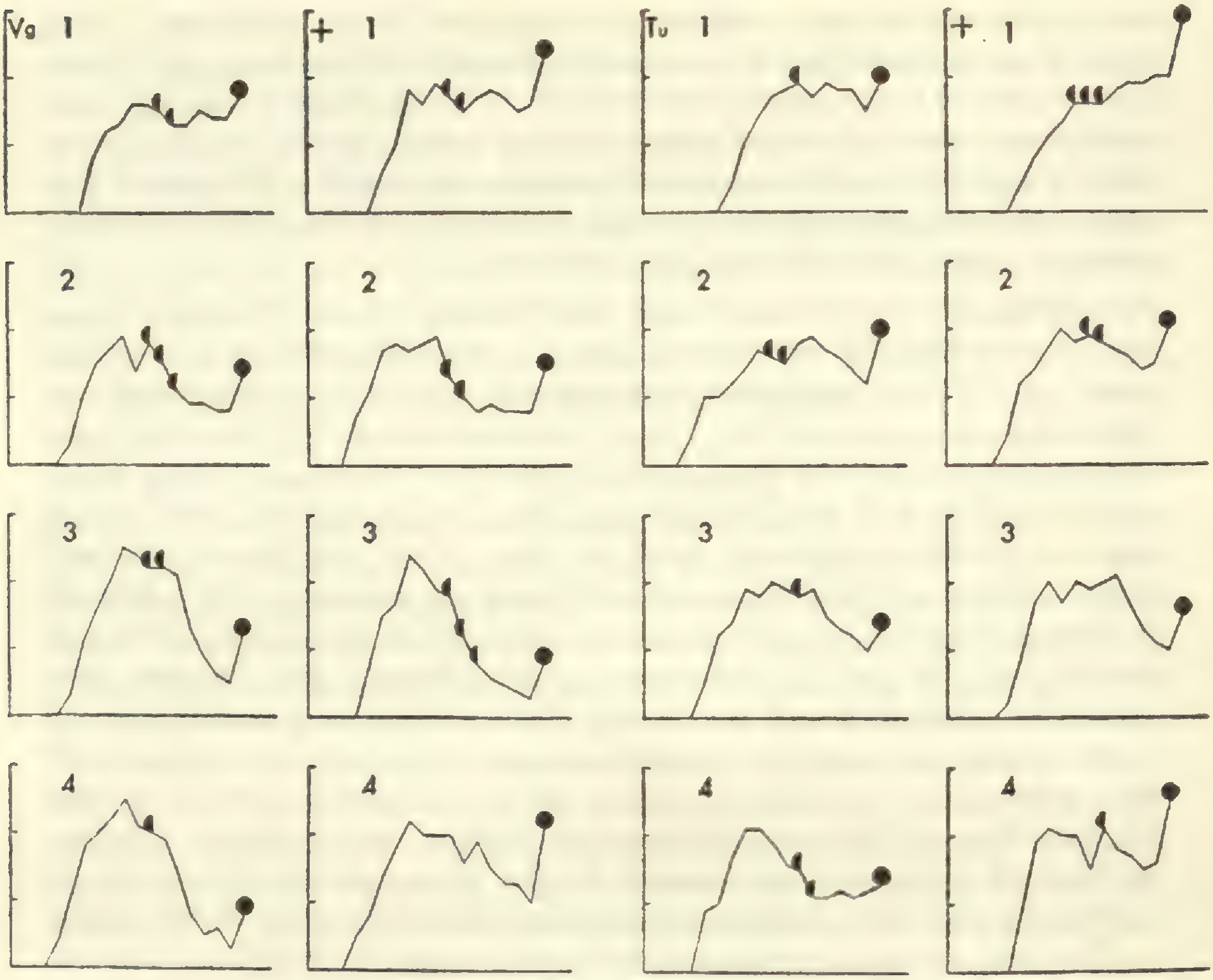

Fig. 2.

Tunicate (Tu). Plants were either normal (+/+) or heterozygous (Tu/+) in genetic constitution. Column "M" in Table III is based on average measurements of 4 mutant-carrying plants, while column "C" figures are for single normal plants. Central spike length is increased in mutant-carrying sibs by doses of 50 and 100 ppm GA. In normal sibs, no reduction in length is noticed until doses reach 150 ppm; this highest dose also shortens central spike length of mutant-carrying sibs, but not as profoundly. Tassel branch numbers are decreased by about half by all doses of GA in mutant-carrying plants; 50 ppm and 100 ppm doses on normal sibs cause great reduction, but 150 ppm doses seem to have little effect. The length of culm over which branches arise is not changed much on both mutant-carrying and normal sibs by any treatments, except that 50 and 100 ppm doses on normals apparently cause some reduction. These two dose levels likewise cause a reduction of peduncle length in normal sibs. Peduncle length in mutant-carrying plants is noticeably decreased only by doses of 150 ppm GA. Ear number is relatively constant for all mutant-carrying sibs, but increased dosages cause decreases in ear formation on normal plants. Internode number of normal sibs is

actually reduced slightly by doses of 150 ppm GA; this same dosage causes more internodes to elongate in mutant-carrying sibs.

Plant heights of normal sibs are not altered significantly by any GA treatments; increases in heights of mutant-carrying sibs were obtained with doses of 50 and 100 ppm, but 150 ppm treatments produced plants whose average lengths were shorter than those of plants subjected to the lower concentrations. Internode diagrams (Fig. 2) show that while normal sibs treated with distilled water show generally increasing internode lengths from base to peduncle; 50 and 100 ppm GA treatments tend to elongate lower internodes and shorten upper internodes. Doses of 150 ppm GA tend to make all internodes long. In mutant-carrying plants, internodes above the ear tend to remain the same length as in water-treated plants. Doses of 50, 100 and 150 ppm progressively make lower internodes longer and upper internodes shorter.

Plate XIV, #2 shows tassels from normal and mutant-carrying sibs. Those treated with distilled water are left of the ruler; those treated with 150 ppm doses GA are at the right. Normal sibs are uppermost, mutant-carrying sibs are lowermost. Reductions in tassel branch number are apparent. Development of silks and large glumes at bases of branches of mutant-carrying sibs are seen. The shorter peduncle is also prominent.

Ramosa-1 (ra_1). Crosses were made so that plants were either heterozygous ($+/ra_1$) or homozygous (ra_1/ra_1) in genetic constitution. In Table III, column "M" represents average measurements of four homozygous plants; column "C" figures are for single heterozygous plants. Central spike lengths were not greatly altered in either homozygous or heterozygous plants, except for some increases in both plant types under doses of 100 ppm GA. 50 ppm doses of GA reduced tassel branch number in heterozygous but not in homozygous sibs. 100 ppm doses were not as effective on heterozygous sibs as were 50 ppm doses, but on homozygotes, a marked reduction of branching was obtained. 150 ppm doses were as effective as 100 ppm doses on heterozygotes, but on homozygotes a reduction in average branch number of more than 50% resulted. The length of culm over which these branches arise was affected by doses of 150 ppm only. This same dosage increased the length in heterozygous plants and decreased the length in homozygous sibs. The final result in each case was nearly identical, a fact borne out by the two tassels on the right in Plate XV, #1. Average peduncle lengths did not differ with treatment in homozygotes, but with heterozygotes, an apparent reduction under 100 ppm doses and 33% increase under 150 ppm doses was obtained.

Ear number in homozygotes was generally reduced by GA treatments, but ears were still the highly branched forms typical for ra_1 (Nickerson and Dale, 1955). The reduction was greatest with 150 ppm GA doses, but all strengths did cause a decrease. In heterozygotes, all GA treatments caused a consistent amount of reduction. Internode number in homozygotes was apparently increased most by doses of 50 ppm GA; higher concentrations reduced this number, but it remained higher than the average for control (water-treated) plants. 100 ppm doses

affected heterozygotes greatest; a reduction below the number present in controls was noted at the 150 ppm level.

GA increased plant heights of homozygotes in a linear relationship to dosage; with the exception of 150 ppm doses, heterozygotes behaved the same way. Even this latter plant, however, was ⅓ higher than its sib which received only distilled water. Internode diagrams (Fig. 3) show that the general pattern exhibited by water-treated homozygotes of increasing internode length up to the ear and further increases for each internode above the ear were simply accentuated for all levels of GA dosage employed. Heterozygous sibs show the same basic pattern with water treatments, with 50 ppm doses and, with some deviation, with 150 ppm doses. Doses of 100 ppm, however, apparently caused many of the internodes produced above the ears to be generally shorter (with one glaring exception) than those preceding them.

Plate XV, #1 shows tassels of heterozygous (upright) and homozygous plants (inverted). The two on the left were treated with distilled water; those on the right with 150 ppm GA. Note reduction in tassel branch numbers and increase in peduncle lengths. Female caryopses were nearly non-existent, on either hetero- or homozygotes.

The strong resemblance of both treated homozygous and heterozygous tassels to control tassels of +/+ plants in Plate XIV should be noted.

Male-sterile 1 (ms_1). Plants were either heterozygous ($+/ms_1$) or homozygous (ms_1/ms_1) in genetic constitution. In Table III, "M" columns are average measurements of four mutant-carrying plants and "C" columns are measurements for single heterozygous normal sibs. Central spike lengths of heterozygous plants were decreased by increasing doses of GA; treatments of 150 ppm caused a 27% decrease. Central spike lengths in homozygous sibs were stimulated by doses of 50 ppm GA, but 100 ppm and 150 ppm doses caused only slight variations from lengths attained by control (water-treated) plants. Tassel branch number, tassel branch area and peduncle length were generally unaffected in both homozygous and heterozygous plants by all GA dose levels; the single deviation in this pattern was the heterozygote under 150 ppm doses, where a 50% reduction in branch number was obtained. Ear number was not reduced in homozygotes except under doses of 100 ppm GA; heterozygotes showed an increase over the control under doses of 50 ppm GA but with higher doses, ear number remained unchanged from that of the control plant.

Internode number of heterozygotes seemed to be increased slightly by 50 and 100 ppm doses. Homozygotes showed a definite increase in number of measurable internodes over control plants with all GA treatment levels.

Plant heights of homozygotes were increased by 50 and 100 ppm doses, but 150 ppm doses did not increase them further. Heterozygotes were relatively unchanged by all GA levels except 150 ppm which caused about a 10% increase in height. Internode diagrams (Fig. 3) show that heterozygotes have a series of internodes that increase rather rapidly and then form a relatively flat plateau with

a slight increase in the peduncle. 50 ppm doses of GA affect later-formed internodes so as so give a series of continually longer internodes from base to tassel. 100 ppm doses increased earlier internode lengths over those shown in controls. 150 ppm doses exaggerated early internode lengths and shortened later ones up to the peduncle, which is about as long as that of the control plant. Curves for homozygotes carrying the mutant show strong similarity in control plants to heterozygotes. 50 ppm doses show no marked changes, but 100 ppm doses tend to accentuate lengths of early internodes and shorten lengths of later-formed ones. This trend is even more pronounced under doses of 150 ppm. The general curve produced is quite similar to that produced by the heterozygote under similar treatment.

Plate XV, #2 shows tassels from heterozygous (upper) and homozygous (lower) plants. Two are from plants treated with distilled water (left of ruler) and two from plants treated with 150 ppm GA (right of ruler). The general reduction in tassel branch number and wider spacing of spikelets on branches is apparent. However, no pollen was shed by homozygotes treated with GA. Three female caryopses with silks were developed at the base of the lowest branch of one mutant-carrying tassel in the five which were collected. Their development in other tassels not harvested was just as scarce.

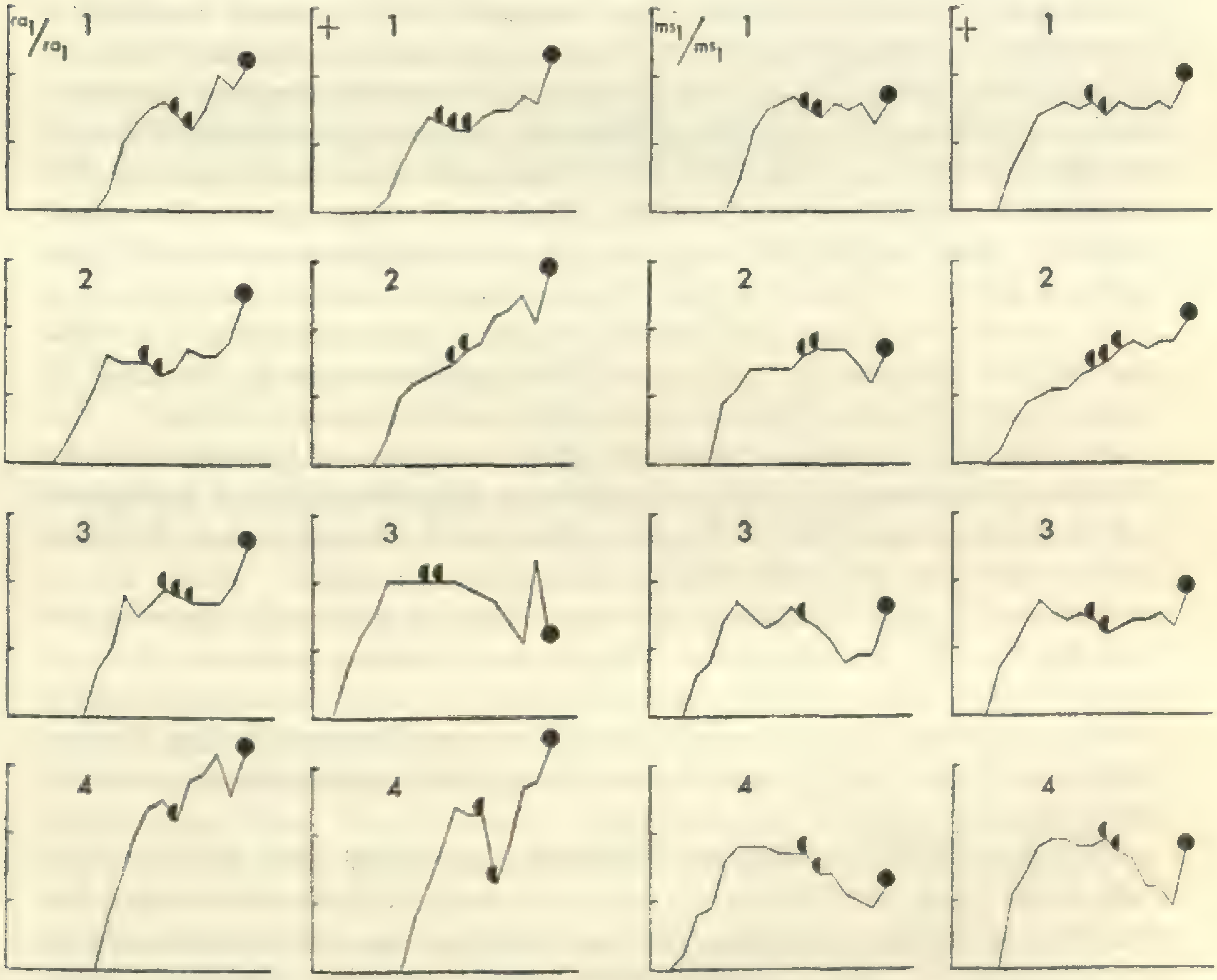

Fig. 3.

Discussion and Conclusions

Nickerson and Dale (1955) described certain morphological characters of sixteen tassel mutants. Some of these have been subjected to treatments with GA; it is planned to treat the remainder during the 1960 growing season.

Plants with genotype ts_2/ts_2 showed no lessening of the gene expression under treatment with GA, but tassels were smaller with increased doses. Expression of Ts_5 was essentially the same under GA treatment. The gene Ts_6 showed several changes in many measurements under GA treatment; resemblances of the tassel in Plate XIV, #2 to untreated ts_4 (Nickerson and Dale, Plate 24, Fig. 2) is remarkable. This gene, however, still is not modified to produce a "normal"-looking or standard tassel under GA treatment.

The genes *Vg* and *Tu* are somewhat opposite in their effects on glume growth. GA reduces their expressions somewhat, so that treated plants have many more normal-appearing glumes than untreated plants. GA-treated *Vg* and *Tu* tassels, however, did not produce much pollen. This male-sterility effect was earlier noted on normal maize plants treated with GA (Nelson & Rossman, 1958; Nickerson, 1959). Female caryopses were regularly produced in tassels with each of these genes under GA treatment.

The gene ra_1 seems to respond rather completely as far as tassel expression is concerned to GA treatment so that tassels of treated plants closely resemble tassels of normal plants (Plate XV). Ears of ra_1 in this experiment remained characteristically multi-branched structures. This result may be explained simply because GA effects do not last more than 2 or 3 days, and once tassel emergence had occurred GA treatments were stopped. The ear develops mostly after tassel emergence. This fact, coupled with the point that since plants continually grew larger and each cell was therefore proportionately less influenced by successive doses of GA, tended to keep the ears relatively free from any influence of GA. The main effect of GA seen here is apparently the well-known one of restriction of axillary branching in intact plants, a point first noted by Brian (1957).

In male-sterile 1 (ms_1), microspores abort, according to Singleton & Jones (1930) and Emerson *et al.* (1935). GA does not restore the ability of these plants to form pollen grains. Before discussing these results further, a basis for their possible explanation may profitably be introduced at this point.

It is possible that GA depends at least in part for its growth effects on the auxin supply. The maize gene lazy (*la*), known to produce quantities of auxin (van Overbeek, 1938) responds strongly to GA treatment (Nickerson, 1960b). Brian and Hemming (1958), Kuse (1958), Galston and Warburg (1959), Wareing (1958) and Weijer (1959) have all postulated a positive auxin-gibberellin relationship in a variety of plants and plant parts.

The effects of GA on these maize mutants may depend upon the amount of auxin in the plant part affected at a particular time. If it may be assumed that developing male florets produce auxin in an increasing rate which reaches a peak and then drops off rapidly shortly before anthesis, and that developing female

florets produce far greater quantities much quicker, and for a longer time but later in the life of the plant, then one could postulate the following relationship. As the tassel of a normal (+/+) plant begins its development, the peduncle receives elongation stimulus (auxin) in greatest quantity first. However, the amount of auxin produced by the tassel quickly reaches the level above which stem elongation ceases. Thus the peduncle matures early (Murdy, 1960), and the lowermost internodes elongate and mature from the base up as the auxin concentration from above rapidly increases and then decreases. The ear-shoot (an axillary bud) is stimulated by the high point of auxin concentration reached; it then begins to develop and forms silks rapidly. About the time silks are extruded, the auxin supply from the tassel diminishes toward zero. Under the influence of a diminishing auxin supply, the internodes below the peduncle but above the ear, heretofore inhibited by a high auxin concentration, finish their elongation and mature. Brace roots develop at the lower end of the culm, again as the auxin supply falls below the optimum for stem growth. Shortly thereafter, the pollinated ear produces quantities of auxin which quickly results in an excess over optimum for either stem or bud development; the internodes of the ear shoot or shank thus do *not* elongate. In many forms, the shank never fully matures, producing a structure which bends easily under the weight of the developed ear.

There are, then, the following general patterns of growth which conform to the above hypothesis concerning auxin concentrations and GA effects. Tassel-seed 2, normally a producer of quantities of female caryopses in the tassel, has its lower internodes longer than those of normal plants and its upper ones shorter than those of normal plants. In Tassel-seed 5, the first third of tassel florets differentiated are female (bases of central spikes and lower tassel branches) and all later-formed ones are male. In Tassel-seed 6, the reverse is true; the first third of spikelets in the same tassel locations are male and all outer (and later) ones are much-proliferated short branches of poorly-developed female florets.

Gibberellic Acid treatment accelerates both the early rise and the later dip in ts_2 (Fig. 1). Presumably auxin concentration rapidly reached inhibitory levels for stem elongation. In Ts_5, the rise in lengths of internodes in control plants is followed by a leveling-off (Fig. 1); subsequent GA treatments accentuate the lengths of those internodes above the ear, formed when most auxin was produced by male florets. Peduncle lengths (here formed under amounts of auxin from female florets) were always shorter than these elongated upper internodes. In Ts_6, (Fig. 1) a long peduncle and a steep rise in early internode length (formed under amounts of auxin from male florets) was always followed by a decline in length of internodes above the ear (formed under amounts of auxin from female florets) in control plants. GA accentuates the early rise but does not affect the decline pattern above the ears except to make all internodes slightly but uniformly longer. In *Vg*, (Fig. 2) an internode length is reached rapidly which decreases only slightly with a slight increase in the peduncle length. The effect of GA is to accentuate the early increase and cause marked declines in internode lengths above

the ear, with the earlier-formed peduncle length showing a final strong increase. Since the stamens of *Vg* dry out and die before anthesis, the late supply of tassel auxin is presumably cut off. *Tu* (Fig. 2) follows the same pattern but GA effects are less pronounced. Ramosa-1 (ra_1, Fig. 3) has an internode pattern of general increase in length from base to tip; here all florets remain male, but they are quite numerous and shed pollen over a much longer period than do normal plants. GA treatment accentuates this pattern but preserves its general form.

In ms_1 (Fig. 3) a sharp initial increase in internode length is followed by leveling-off with only a slight dip before the peduncle. GA accentuates both the early rise and the late dip. The fact that microspores form but then degenerate before anthesis with possible consequent severe decrease in tassel auxin production would account for the GA behavior if it depended upon auxin concentration for its elongation effects.

Confirmation of many points in the above discussion must occur before it will satisfy critical investigators. It may, however, be suggested that not only does GA apparently depend upon the presence of auxin for its elongation effects, but it also depends upon the particular concentration of auxin (and GA) available in the elongating cells. A possible point in favor of this hypothesis is that it seemingly explains the effect of GA upon the dwarf gene *nana* (na_1); Phinney (1956) reported it as "not responding to GA treatments". Van Overbeek (1935) had previously shown that although *nana* made even more than normal amounts of auxin, the material was destroyed before it diffused down the culm. If there were no auxin, then GA, which presumably depends upon its presence for at least part of its effects, would cause no such effects. There are some facets of GA effects not explained by this proposal, but elongation effects in maize may reasonably be regarded in this manner.

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The author wishes to thank Dr. M. V. S. Raju for his skill in preparing Figs. 1–3 and Dr. F. W. Went for kindly consenting to review the manuscript.

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TABLE I

PLANTING AND TREATMENT DATA OF SEVEN MAIZE MUTANTS

Mutant	Planting Date (1959)	Date of first GA treatment	Total number of plants treated	Date of last GA treatment	Total number of treatments	Total Amounts of GA applied in micrograms		
						50 μg per dose	100 μg per dose	150 μg per dose
ts_2	15 June	6 July 1959	86	14 August 1959	fourteen	700 μg	1400 μg	2100 μg
Ts_5	16 June		104					
Ts_6	16 June		96					
Vg	14 June		107					
Tu	14 June		126					
ra_1	12 June		87					
ms_1	15 June		117	26 August	18	900 μg	1800 μg	2700 μg

TABLE II

RESULTS OF GA TREATMENT ON CERTAIN MEASUREMENTS OF THREE MAIZE TASSEL-SEED GENOTYPES AND THEIR NORMAL SIBS

Genotype	Dosage of GA in micro-grams	Length of central spike (cm.)		Number of primary tassel branches		Length of tassel branching area (cm.)		Peduncle length (cm.)		Plant height (cm.)		Number of internodes		Number of ears	
		M	C	M	C	M	C	M	C	M	C	M	C	M	C
$M = ts_2/ts_2$ (single plant measurements)	0	27		15		10		11		171		14		4	
	50	16		12		8		5		182		15		2	
	100	20		8		8		7		182		15		2	
	150	12		13		5		5		203		15		1	
$M = Ts_5/+$ (av. of 4) $C = +/+$ (single plant measurements)	0	26.5	26	11	21	8.5	13	15	22	168	172	11.5	11	1.2	2
	50	30.5	30	6	14	7	14	11.5	26	177	202	12.5	13	2	4
	100	18	28	12	14	10.5	13	14.2	21	205	236	12.5	13	1.7	1
	150	27	24	8	14	7.5	15	18.5	26	240	231	13	13	2.2	1
$M = Ts_6/+$ (av. of 4) $C = +/+$ (single plant measurements)	0	12	35	15	14	10.2	13	25	29	167	225	13	14	1.2	2
	50	9.5	27	16	13	11	13	12	23	202	226	15	13	0.5	2
	100	9.5	32	18	8	15	10	14	17	217	241	15.5	15	0.5	2
	150	11	27	21	9	15.5	16	21	24	240	255	15	13	0.7	1

TABLE III

RESULTS OF GA TREATMENT ON CERTAIN MEASUREMENTS OF FOUR MAIZE TASSEL GENOTYPES AND THEIR NORMAL SIBS

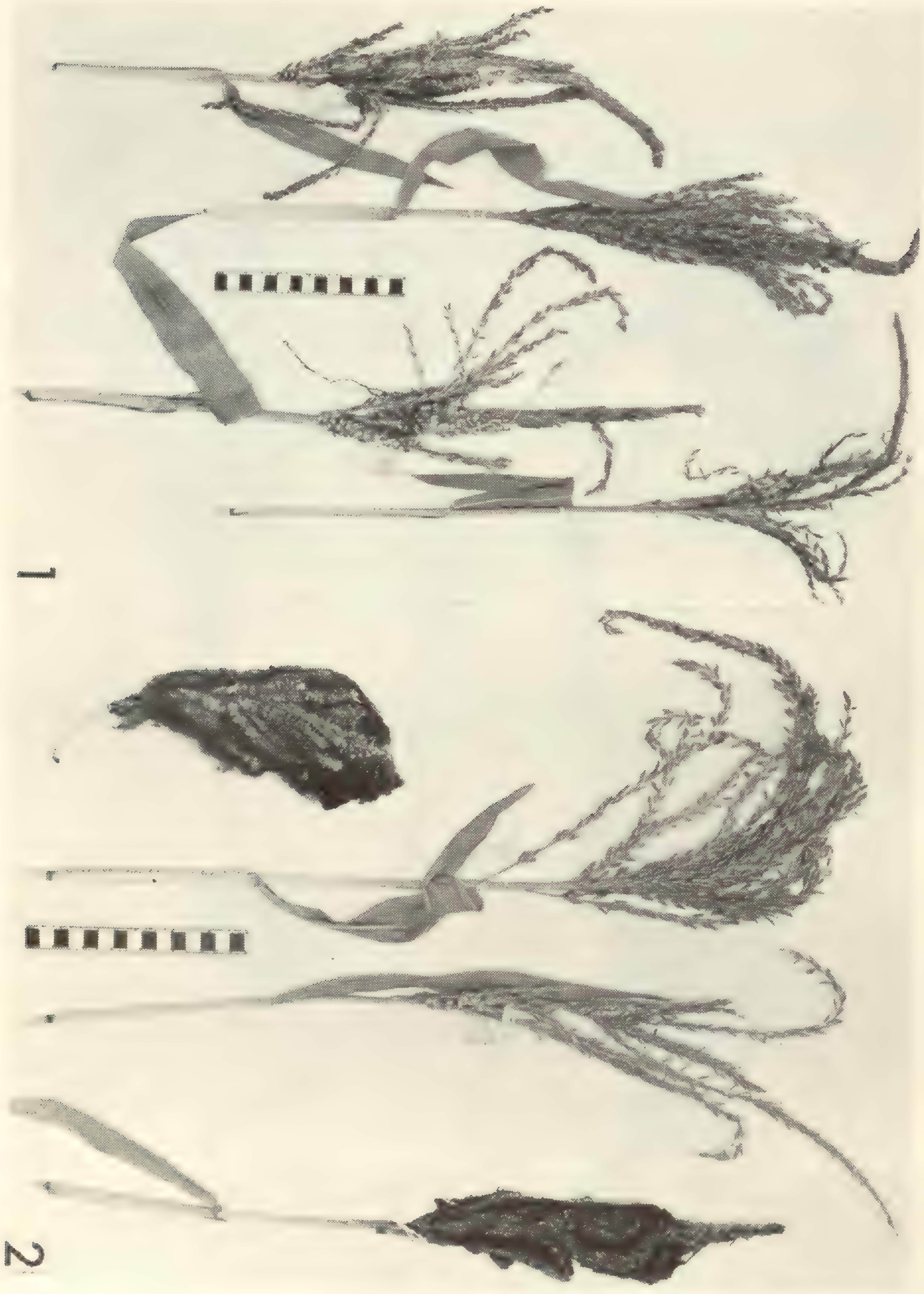
Genotype	Dosage of GA in micro-grams	Length of central spike (cm.)		Number of primary tassel branches		Length of tassel branching area (cm.)		Peduncle length (cm.)		Plant height (cm.)		Number of internodes		Number of ears	
		M	C	M	C	M	C	M	C	M	C	M	C	M	C
M = Vg/+ (av. of 4) C = +/+ (single plant measure-ments)	0	28	31	14	15	10	12	17.5	23	178	207	12.5	13	1.2	2
	50	14.5	28	18	9	10	9	13	14	155	185	14	15	2.2	2
	100	23.5	24	9	10	11	10	16	8	238	168	14	14	2	3
	150	15	25	10	10	12	13	9	21	218	234	15	15	4	0
M = Tu/+ (av. of 4) C = +/+ (single plant measure-ments)	0	22.5	28	21	14	13	14	17	28	176	208	11.5	13	1.2	3
	50	27	28	10	5	12	9	18	20	196	204	14	13	1.7	2
	100	28	30	13	6	13	9	14	15	203	211	13.5	14	1.2	1
	150	15	9	12	14	10	14	12	25	190	216	13	12	1.2	1
M = ra_1/ra_1 (av. of 4) C = $+/ra_1$ (single plant measure-ments)	0	11	21	64	18	31	13	23	22	155	170	11	13	2.7	3
	50	9	28	63	10	32	12	23	28	196	222	13	13	1.7	2
	100	15	30	39	14	30	10	24	11	213	256	12	15	1.7	2
	150	11	25	25	13	17	20	25	33	236	229	11.5	11	1.2	2
M = ms_1/ms_1 (av. of 4) C = $+/ms_1$ (single plant measure-ments)	0	15	22	10	14	7	9	15	19	166	202	12.5	14	1.7	2
	50	21	21	8	16	9	10	14	21	181	200	14.5	15	1.7	3
	100	13	20	11	14	8	12	15	18	199	205	15	15	1	2
	150	17	16	8	7	8	9	13	17	199	219	15	14	1.7	2

Explanation of Plate

PLATE XII

Tassels of ts_2/ts_2 maize plants treated with, from left to right; top row, water and doses of 50 ppm GA; bottom row, doses of 100 and 150 ppm GA.

NICKERSON—GIBERELLIC ACID TREATMENT II



NICKERSON—GIBERELLIC ACID TREATMENT II

Explanation of Plate

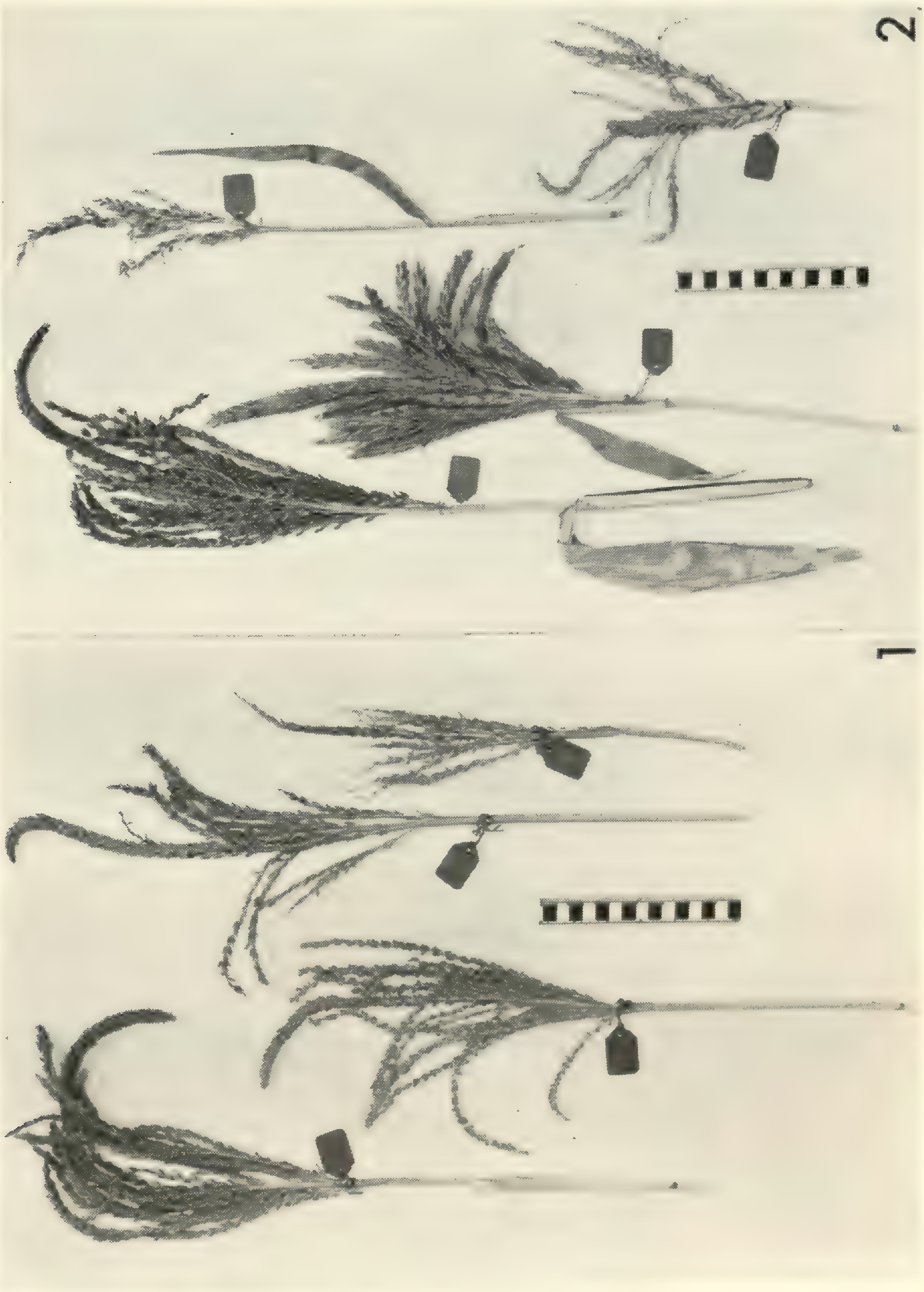
PLATE XIII

Tassels of $Ts_5/+$ (lower) and $+/+$ (1) and $Ts_6/+$ (extreme left and right) and $+/+$ (2) maize plants. Those left of ruler were treated with distilled water; those on right with doses of 150 ppm GA.

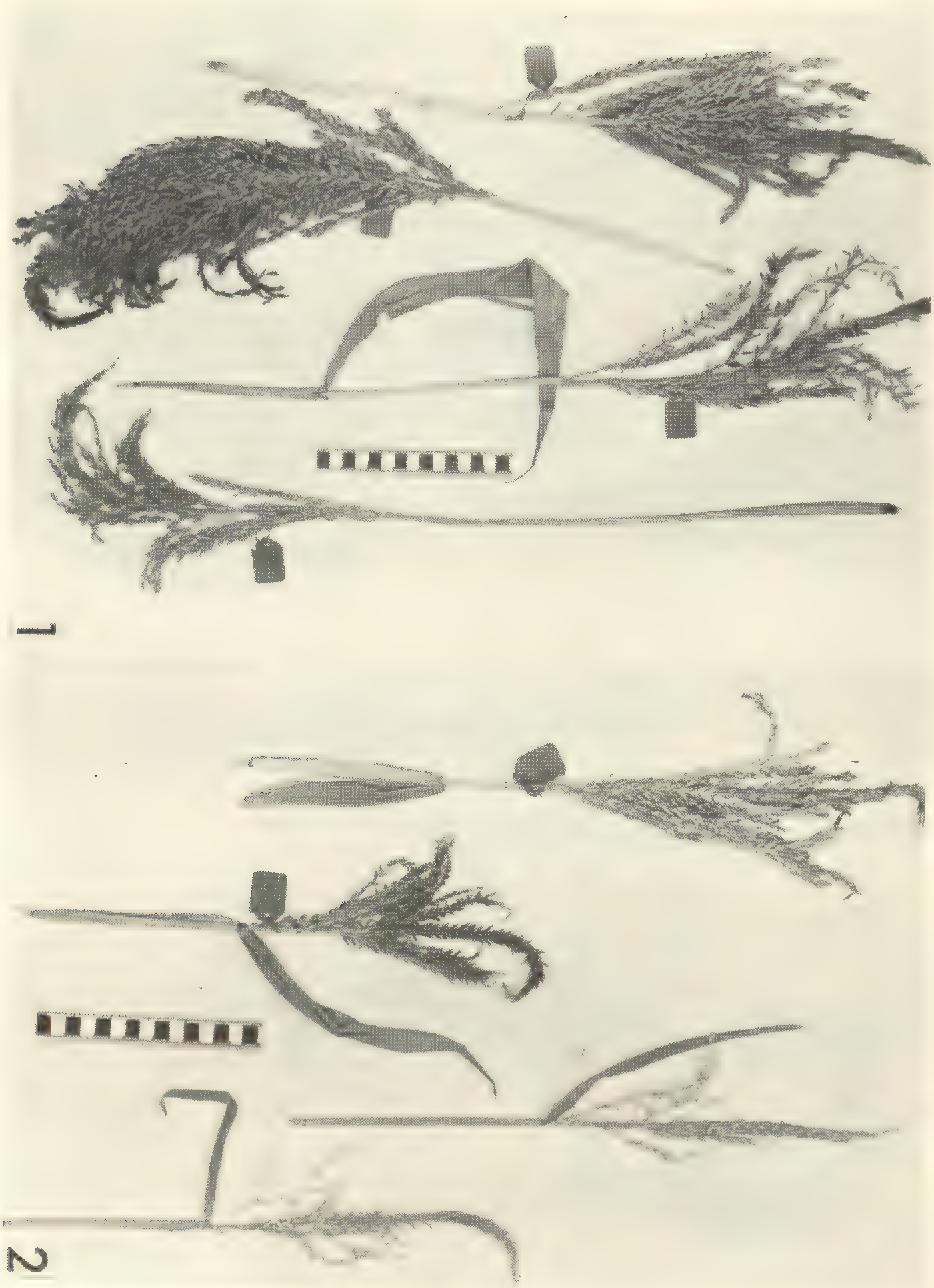
Explanation of Plate

PLATE XIV

Tassels of Vg/+ (lower) and +/+ (1) and Tu/+ (lower) and +/+ (2) maize plants. Those left of ruler were treated with distilled water; those on right with doses of 150 ppm GA.



NICKERSON—GIBERELLIC ACID TREATMENT II



NICKERSON—GIBERELLIC ACID TREATMENT II

Explanation of Plate

PLATE XV

Tassels of ra_1/ra_1 (inverted) and $+/ra_1$ (1) and ms_1/ms_1 (lower) and $+/ms_1$ (2) maize plants. The two tassels at the left in each photograph were treated with distilled water; the two tassels at the right were treated with doses of 150 ppm GA.

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FLORA OF PANAMA

BY

ROBERT E. WOODSON, Jr.

AND

ROBERT W. SCHERY

AND COLLABORATORS

PART IV

Fascicle 3

LORANTHACEAE (C. T. Rizzini)
OPILIACEAE (L. I. Nevling, Jr.)
OLACACEAE (L. I. Nevling, Jr.)
BALANOPHORACEAE (L. I. Nevling, Jr.)
ARISTOLOCHIACEAE (H. W. Pfeiffer)
POLYGONACEAE (J. A. Duke)

ANNALS
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Vol. XLVII NOVEMBER, 1960 No. 4

FLORA OF PANAMA

Part IV. Fascicle 3*

LORANTHACEAE

By CARLOS TOLEDO RIZZINI

Vines, undershrubs, shrubs or rarely trees, always parasitic on roots or stems; the vines, less commonly the shrubs, bearing adventitious roots united with their hosts. Leaves usually opposite, sometimes alternate, entire, seldom reduced to scales, more or less coriaceous and inconspicuously nerved, the nervation either palmate or pinnate; without stipules. Flowers very large to minute, frequently showy because of the bright colors, androgynous or unisexual, spicate, clustered, strobilate or arranged in ternations, these in racemes, spikes, corymbs, umbels and so on, rarely solitary, subtended by bractlets either free or coalescent, or bractless; perianth simple or double; calyculus present or absent; tepals (perianth segments) 3–6 or none; stamens as many as the tepals, reduced to staminodia in the pistillate flowers, the filaments joined to the tepals; pollen grains variable, globose or triangular, the exine either smooth or granulose (in some small genera it is reticulate or aculeate); ovary formed by the receptacle or blossom axis (thus the above mentioned calyculus is the edge of the receptacle), 1–(rarely several)-celled, sterile and poorly developed in the staminate flowers; stigma capitate, wanting in the male flowers which, however, have a slightly reduced style. Fruit (indeed a pseudofruit since it is developed from the receptacle), so far as American species are concerned, a berry (a drupe in certain Old World forms), frequently showing a milky layer containing rubber and persistent perianth parts; seed solitary, naked, the endosperm obviously developed and fleshy, rarely lacking; embryo small, with 2 rather large cotyledons.

The plants of this family are either completely (when they are leafless and without chlorophyll) or partly (when they bear normal foliage leaves) parasitic on other woody plants. The roots applied to the host become haustoria and through these part or all the food supply is secured from the latter. The few erect, terrestrial, tree-like forms live upon roots and their haustoria are underground.

The family comprises about 38 genera and 1,400 species, mainly tropical and subtropical but occasionally found in temperate regions. It is very homogeneous,

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yet the morphological types are well marked so that the New World forms are readily distinguishable from the Old World ones. The Central American species are more closely related to the South American than to the North American or West Indian ones.

The following artificial key to genera serves only for the Panamanian entities so far known, since it has been prepared with the purpose of making the generic identification easy.

a. Flowers small to very large, at least 2 mm. long, not immersed in the rachis of the inflorescence.
  b. Plants terrestrial. Bractlets large, foliaceous, free. .... 1. Gaiadendron
  bb. Plants growing upon others. Bractlets minute, mostly coalescent.
    c. Flowers very small, hidden inside short, long-bracted spikes, the male flowers naked. Pollen grains spherical, prominently aculeate. 2. Antidaphne
    cc. Flowers perianthed, freely inserted, conspicuous. Pollen grains neither round nor aculeate.
      d. Flowers several cm. long, showy, each subtended by a cupula or cup. Endosperm wanting. .... 3. Psittacanthus
      dd. Flowers up to 1 cm. long, usually shorter, without a cup below the calyculus. Endosperm present.
        e. Flower perfect, each subtended by one bract plus two bractlets, all closely united. .... 4. Phrygilanthus
        ee. Flowers unisexual (the vestigial pistil remains in the staminate flowers as the pollenless anthers do in the pistillate ones), each set of bract and bractlets subtending three flowers (ternation).
          f. Filaments of the stamens slender and thin. Pollen grains dimorphous: the fertile triangular and tricolpate mixed with sterile, globose and smooth ones. .... 5. Struthanthus
          ff. Filaments of the longer stamens scalloped at each side. Pollen grains belonging to one type, triangular. .... 6. Phthirusa
aa. Flowers very small, no longer than 2 mm., sunken in depressions in the rachis of the spike.
  b. Calyculus distinct though poorly developed. Tepals 6. Pollen grains reticulate. .... 7. Oryctanthus
  bb. Calyculus lacking. Tepals 3. Pollen grains smooth.
    c. Anther 1-celled, dehiscing transversely. .... 8. Dendrophthora
    cc. Anther 2-celled, opening by 2 longitudinal slits. .... 9. Phoradendron

1. GAIADENDRON G. Don

Gaiadendron G. Don, Gen. Hist. 3:431. 1843; Eichler, in Mart. Fl. Bras. 5, pt. 2: 47. 1868 (as a subgenus of *Phrygilanthus*).

Tall shrubs or small trees living upon earth, but parasitizing roots of other plants. Leaves opposite, more or less coriaceous, almost always minutely, but evidently, punctate beneath. Flowers conspicuous, colored, 4–8-merous, perfect, in ternations, these in racemes or corymbs; bractlets conspicuously developed, free, persistent; pedicels often unequal. Pollen grains 3-angled, the exine granulose. Ovary said to be 2–6-celled, but this scarcely convincing. Fruit baccate, the seeds albuminous.

A chiefly Andean genus of about 6 species. The following is the only known from Central America, where it is endemic. A careful re-examination of the ovary, living or fixed, will probably show that the genus does not essentially differ from *Phrygilanthus* and that it must be retained, as by Eichler, under the last mentioned name.

1. Gaiadendron poasense Donn. Sm. in Bot. Gaz. 56:61. 1913.

Parasitic shrubs or short trees reported to reach a height of 3–6 m., growing on the ground, with erect, terete branches. Leaf blades slightly ovate or oblong, acutish at the base, attenuate to the blunt apex, minutely punctate beneath, fleshy-coriaceous, often drying revolute at the margins, nerveless, to 8 cm. long and 4.5 cm. wide; petioles 5–10 mm. long. Racemes axillary, solitary, 7–10 cm. long. Bractlets ovate, persistent, foliaceous, 5–12 mm. long. Flowers in ternations, the

Fig. 72. *Gaiadendron poasense*

lateral short-pedicelled, androgynous, about 15 mm. long; tepals 6–7 in number, 13 mm. in length. Ternations pedicellate, the pedicels about 4–6 mm. long. Fruit not found yet.

Costa Rica, Panama.

CHIRIQUÍ: Volcán de Chiriquí, *Terry 1311*; *Davidson 995*; vicinity of Cerro Punta, *Allen 1518*; Boquete, Bajo Chorro, *Davidson 44*.

2. ANTIDAPHNE Poepp. et Endl.

ANTIDAPHNE Poepp. et Endl. Nova Gen. ac Spec. 2:70. 1838.

Stachyphyllum Van Tieghem, in Bull. Soc. Bot. France 42:565. 1895.

Medium-sized, erect shrubs, without adventitious roots in the shoots. Leaves alternate, thickly coriaceous. Flowers minute, spicate, dioecious; spikes short (up to 10 mm. in length), sessile in the leaf axils, more or less strobiliform; bractlets scale-like, broadly imbricate, either caducous or persistent in anthesis. Staminate flowers reduced to 3–6 stamens inserted at the base of the bractlets on a small disk, the filaments elongated, unequal; anthers erect, 2–4-celled, longitudinally dehiscent; pollen grains globose, with 3 pori, the exine conspicuously aculeate. Pistillate flowers sessile, in groups of 2–5 at the bractlet axils, bearing a perigonium; tepals well or poorly developed, adnate to the ovary; style none, but the stigma capitate. Fruit a round berry, the pericarp fleshy and possessing an evident milky layer.

A distinctive genus amongst South American Loranthaceae, recognized at first glance by the minute, bracteate, compact and dioecious spikes bearing naked male flowers; moreover, another striking feature lies in the aculeate (echinate) round pollen grains, since no other genus in the family shows such a character.

Most peculiar too is the geographical distribution of the 4 known species. *A. viscoidea* Poepp. et Endl., the commonest of all, is Andean; *A. fendleri* (V. Tiegh.) Engler occurs in Venezuela not rarely; *A. amazonensis* Rizz. and *A. paraensis* Rizz., both more recently detected and described, are from the Amazonian forest. Thus the 4 species behave as being vicarious, coming down from the high Andean mountains to the low Amazonian basin, the habitats never intergrading with one another.

Keeping in mind the aforesaid statement, it is somewhat surprising to find *A. viscoidea* in Central America (Costa Rica, Guatemala and Panama) but—it must be stressed—at high altitudes (from 1,400 m. upwards).

1. ANTIDAPHNE VISCOIDEA Poepp. et. Endl. Nova Gen. ac Spec. 2:70. 1838.

A densely branched shrub, glabrous, the branches generally to 50 cm. long, terete or nearly so. Leaves almost sessile, or the petioles very short and thick, obovate to suborbicular, cuneate at the base, the nerves very prominent and openly reticulate, coriaceous, 3–7 cm. long, 2–3 cm. wide. Flowers cream-colored, the Perianth segments slightly dentate. The bractlets fall when the flowers open. Fruit oval.

This species differs from the others mainly in having shorter spikes covered with bractlets which are deciduous by the time of anthesis. The whole genus is worked out in Rodriguesia 18–19:221–225, *pl. 26–28.* 1956.

Steyermark mentions a collection (Fieldiana, Bot., 24. pt. 4:63. 1946) in Panama; it certainly is very rare there; no specimens were seen.

3. PSITTACANTHUS Mart.

PSITTACANTHUS Mart. in Flora 13:106. 1830; Eichler, in Mart. Fl. Bras. 5 pt. 2:23. 1868.

Always stout and erect shrubs, lacking aerial roots. Leaves usually opposite, coriaceous. Flowers large, showy, brilliantly colored, hexamerous, androgynous, in ternations or binations; these in racemes, corymbs or umbels; bractlets united in a cup which subtends the flowers. Tepals either free or connate, sometimes ligulate at the base. Stamens unequal, alternately shorter and longer, the filaments slender; pollen grains 3-angled, flattened, the exine granulose. Stigma capitate. Fruit baccate, large for the group, the seeds without endosperm but bearing big, and often more than 2, cotyledons.

About 80 species are known, especially in tropical America, 5 of them reported from Panama. The genus is easy of recognition because of the cups subtending the flowers, which are the largest among Loranthaceae, at least the New World ones.

a. Branches terete. Leaves not falcate. Flowers 2–4 cm. long.
  b. Leaves very broadly ovate, approaching orbicular, up to 9.5 cm. in width .... 1. P. SCHERYI
  bb. Leaves not ovate, to 3 cm. broad.
    c. Leaves oblong. Perianth 2–3 cm. long, the tepals lacking a typical ligule .... 2. P. LATERIFLORUS
    cc. Leaves obovate-elliptic. Perianth 3–3.5 cm. long, the tepals conspicuously ligulate at the base .... 3. P. ALLENII
aa. Branches 4-angled. Leaves oblique. Flowers 3–9 cm. long.
  b. Leaves lance-elliptic or oblong, obtuse. Flowers 3–5 cm. long .... 4. P. CHRISMARII
  bb. Leaves mostly ovate, acute. Flowers 5–9 cm. long .... 5. P. SCHIEDEANUS

Another species that may well be expected is *P. calyculatus* (DC.) Don, from Mexico and found in Costa Rica, which is closely allied to *P. chrismarii* Urban but distinguishable by the longer, acute and not oblique leaves.

1. PSITTACANTHUS SCHERYI Woods. in Ann. Missouri Bot. Gard. 28:426. 1941.

A very stout shrub up to 1.8 m. tall. Branches terete, glabrous, very thick. Leaves widely ovate or suborbicular, the rounded base scarcely contracted to the petiole, fleshy-coriaceous, the nerves poorly developed, 9–11 cm. long, 6–9.5 cm. broad; petioles about 8 mm. long. Flowers orange below, deep yellow toward the tips, 2.5–3.2 cm. long; the 2-flowered peduncles fasciculately disposed, 3–6 mm. long; pedicels about 5 mm. long; calyculus with entire margin, 2.5 mm. deep; cup about as long as the calyculus; perianth segments slightly enlarged at the base, the filaments attached above the middle.

Endemic.

CHIRIQUÍ: vicinity of Bajo Mona and Quebrada Chiquero, *Woodson & Schery 581* (type).

2. Psittacanthus lateriflorus Woods. & Schery, in Ann. Missouri Bot. Gard. 27:309. 1940.

A slender and handsome shrub, drying olivaceous. Branches terete, glabrous. Leaves oblong or elliptic, attenuate both to the blunt apex and acute base, in youth more or less spatulate, firmly coriaceous, nerveless or nearly so, 4–7 cm. long, 1.5–2.5 cm. wide; petioles 2–5 mm. long. Flowers geminate 2–6 in each axil, corymbosely disposed, scarlet, 2–3 cm. long; common peduncle about 8 mm. long, the pedicels twice as short; calyculus and cup with entire margins, 2 mm. long; perianth segments lightly dilated at the base, the filaments medially inserted. Fruit green, ellipsoid, 6 to 12 mm. long.

Endemic.

canal zone: road to San Carlos, *Harvey 5173*. coclé: vicinity of El Valle de Antón, *Allen 1979* (type); in the same place, *Allen 3702* and *2233*; marshes along R. Antón, *Hunter & Allen 371*.

3. Psittacanthus allenii Woods. & Schery, in Ann. Missouri Bot. Gard. 27:309. 1940.

In habit and color very similar to *P. lateriflorus* Woods. & Schery, but the flowers are usually longer and broader and the tepals bear well developed ligules. Branches terete, toward the tips somewhat compressed. Leaves elliptic-obovate, rounded at the apex, cuneate to the base, coriaceous, almost nerveless, 4–7 cm. long, 2–3 cm. broad; petioles 2–3 mm. long. Flowers 2–6 corymbosely arranged, orange, 3–3.5 cm. long; common peduncle about 5–8 mm. long; pedicels 5 mm. long; calyculus and cup with entire margins, 1–2 mm. long; perianth segments or tepals dilated at the base, showing conspicuous ligules; filaments about medially attached. Fruit not seen.

Endemic.

coclé: vicinity of El Valle de Antón, *Allen 1223* (type); Penonomé, *Williams 526*.

P. lateriflorus and *P. allenii* are easily confused, and difficult to separate, at first glance. The ligule, which the latter bears, is to be seen as a basal outgrowth of the perianth segments; one must seek for it at the inner portion of the tepal base, which is dilated about 2 mm. upwards. Moreover, the leaves of *P. allenii* show a well-marked tendency to be broader toward the apex.

Davidson's bad specimen no. *568* (Boquete, Chiriquí) differs from *P. allenii* in no wise but the leaf shape, which is lanceolate.

4. Psittacanthus chrismarii Urban, in Engl. Bot. Jahrb. 24:331. 1897.

Psittacanthus americanus (L.) Mart. in Flora 13:108. 1830, as to the Mexican and Central American specimens, not the West Indian ones.

Plants erect, the branches quadrate and glabrous. Leaves subsessile (petioles 0–3 mm. long), obliquely lance-elliptic or oblong, rarely ovate, narrowed both to the blunt apex and acute base, thick and hard, faintly 3–6-nerved, 7–12 cm. long, 2–4 cm. wide. Inflorescences densely flowered, both axillary and terminally

Fig. 73. *Psittacanthus allenii*; below: base of tepal in profile, showing ligule.

racemose or paniculate, 8–15 cm. long; common peduncle to 2.5 cm. long; pedicels about 1.5 cm. long; cups 1–2 mm. deep. Buds conspicuously clavate-apiculate, to 4 cm. long. Flowers red, 3–5 cm. long, in ternations; calyculus denticulate at the margin, 3–4 mm. long; perianth segments enlarged at the base, the filaments about medially adnate.

CHIRIQUÍ: El Boquete, *Maxon 538*. COCLÉ: vicinity of Las Uvas, *Allen 2796*; Aguadulce, *Pittier 4836*. HERRERA: Pesé, *Allen 806*. PANAMÁ: vicinity of San Carlos, *Allen, 1130, Harvey 5172*.

P. chrismarii Urban has always been confused with *P. americanus* (L.) Mart., from the West Indies; nevertheless, as Urban pointed out, it is easily distinguished by the obviously 4-angled branches.

5. Psittacanthus schiedeanus (Cham. & Schl.) Bl. in R. & S. Syst. 7, pt. 2: 1730. 1830.

Loranthus schiedeanus Cham. & Schl. in Linnaea 5:172. 1830.

Stout plants with thick, 4-angled, compressed branches, the branchlets often wing-margined. Leaves falcately ovate, rarely oblong, acute, rounded at the base, coriaceous, the nerves slightly impressed, to 13 cm. long, about 3–5 cm. wide; petioles 1–1.5 cm. long. Inflorescences corymbose, terminal, very densely flowered, up to 20 cm. long; common peduncle to 4 cm. long; pedicels about 2 cm. long; bracts well developed, 5–12 mm. long; cups mostly 2 mm. deep. Buds slightly clavate, briefly apiculate. Flowers yellowish-orange, 5–9 cm. long, in ternations; calyculus irregularly denticulate, 5 mm. long; perianth segments not enlarged at the base, the filaments medially attached.

Mexico and Central America.

chiriquí: Finca Lérida to Peña Blanca, *Woodson & Schery 308*; R. Chiriquí Viejo, *G. White 76* and *P. White 331, 42*; Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 915*; vicinity of Bajo Mona and Quebrada Chiquero, *Woodson & Schery 596*; trail from Cerro Punta to headwaters of Río Caldera, *Allen 1444*.

4. PHRYGILANTHUS Eichl.

Phrygilanthus Eichl. in Mart. Fl. Bras. 5, pt. 2:45. 1868.

Shrubs or small trees living both on earth, as root parasites, and upon other woody plants. Leaves generally leathery, opposite, rarely reduced to scales. Flowers typically hermaphrodite, hexamerous, seldom 4–8-merous, showy, either solitary or arranged in ternations, these in racemes, corymbs or umbels; bracts and bractlets moderately developed, both persistent and caducous according to the species group. Stamens unequal. Pollen grains 3-lobate, the exine granulose. Ovary surrounded by a well-developed, fleshy disk. Fruit a juicy berry, the seeds albuminous.

The genus embraces about 30 species thriving primarily in South American highlands. Only a few have been gathered in Mexico, Central America and Australia. As said before, this genus is poorly distinct from *Gaiadendron* (see both figures) and they possibly will later be joined into one.

1. Phrygilanthus **panamensis** Rizz., n. sp.

Secunda stirps ad Sect. *Martiella* (v. Tiegh.) Engl. attribuenda. A prima species usque adhuc cognita, *Ph. palmeri* (Wats.) Engl. in Mexico vigente, primo vultu floribus racemosis atque foliis caudatis discernitur, neglecta florum magnitudine.

Frutex parasiticus ramis elongatis teretibusque, ad nodos modice incrassatis, internodiis 2–4 cm. longis. Folia ovato-caudata, basi subrotundata, e medio apicem versus gradatim attenuata, extremo apice valde angustata, coriacea, nervis supra tantum subtiliter impressis, 5–9 cm. longa, 3–5 cm. lata; petiolis 1–2 cm. longis. Racemi vulgo 2 ad singulas axillas, longitudine ad 4 cm. usque, laxi, rachidi

Fig. 74. *Phrygilanthus panamensis*

quadrangula; floribus oppositis, neque in ternationibus aggregatis et androgynis. Pedicelli circa 1–2 mm. longi, teretes. Bractea trangulari-acuta, 2 mm. longa; bracteolae duae pro flore, liberae a bractea et hac duplo minores, conformes. Alabastra cylindrica, apice optime apiculata, siccitate nigrescentia. Calyculus ad marginem membranaceum 0.5 mm. altum tantum reductus. Perigonium hexamerum, ad summum 1 cm. longum, caeterum ut in aliis generis speciebus. Fructus latent.

CHIRIQUÍ: Bajo Chorro, Boquete, alt. 1800 m., *M. E. Davidson 431* (US, HOLOTYPE; F, ISOTYPE).

On vegetative characters alone this remarkable plant resembles *Struthanthus marginatus*, with which it has been confused; however, it suffices to observe the pointed buds as well as the solitary flowers at each pedicel of *Ph. panamensis* to make ready distinction.

The only other species of the Section *Martiella* is *Ph. palmeri* (Wats.) Engl., whose leaves rounded at the apex together with its red flowers, to 4 cm. long—not to mention the inflorescence (see Latin diagnosis)—place it far from the above.

5. STRUTHANTHUS Mart.

Struthanthus Mart. in Flora 13:102. 1830; Rizzini, in Rev. Brasil. Biol. 10 (4): 393. 1950.

Shrubs, either erect and rootless or scandent and supplied with adventitious roots, rarely vines. Leaves usually coriaceous. Flowers small, pedicelled or sessile, 5–6-merous, in ternations; these in racemes, panicles, corymbs or spikes, sometimes umbellate; bractlets coalescent or free, persistent or deciduous. Stamens unequal, the filaments slender. Pollen grains of two types: fertile 3-lobate, the exine granulose; sterile globose, the exine smooth. Pistillate flowers with staminodia; staminate ones with reduced style, this lacking stigma. Buds of the staminate flowers clavate. Stigma capitate. Fruit a berry, the seeds with endosperm.

The genus consists of about 60 species, mostly South American. Only a few have been recorded in Mexico and Central America.

a. Leaves acuminate.
- b. Spikes showing numerous imbricate scales at the base. Ternations sessile without bractlets (they are promptly caducous) .... 1. S. polystachyus
- bb. Spikes naked at the base. Ternations pedicellate with persistent and connate bractlets .... 2. S. marginatus

aa. Leaves rounded at the apex.
- b. Ternations without bractlets (they are soon deciduous). Flowers short-pedicelled .... 3. S. orbicularis
- bb. Ternations bearing connate bractlets. Flowers sessile, the ternations stalked .... 4. S. rotundatus

1. Struthanthus polystachyus (R. & Pav.) Bl. in R. & S. Syst. 7, pt. 2:1731. 1830.

Loranthus polystachyus R. & P. Fl. Peruv. 3:50. 1802.

An erect shrub lacking adventitious roots, as much as 2 m. high (usually shorter). Branches terete, the branchlets rather compressed. Leaves broadly ovate or almost oblong, acuminate, rounded at the base, veined on both sides, more or less coriaceous, cartilaginous-margined, to 15 cm. long, 7 cm. broad; petioles 1–2 cm. long. Ternations completely sessile. Spikes solitary or 2–3 together, 3–5 cm. long. Inside the foliar axils there are many imbricate scales (prophylls) enclosing the base of the spikes. Bractlets soon caducous and so not detectable. Flowers yellow, 3–4 mm. long. Fruit oval, blue, 5–6 mm. thick; fruiting spikes rather longer and thicker than the flowering ones, to 7 cm. long.

South and Central America (however, not yet found in Brazil). An easily recognizable species.

Bocas del Toro: *von Wedel 480*; Río Cricamola, *Woodson, Allen & Seibert 1911*. Coclé: north of El Valle de Antón, *Allen 3721*; mountains beyond La Pintada, *Hunter & Allen 624*; Almirante, *Cooper 205*; Bismarck, *Williams 561*. Colón: along Río Fató, *Pittier 4192*. Veraguas: vicinity of Sta. Fé, *Allen 4391*.

2. STRUTHANTHUS MARGINATUS (Desr.) Bl. in R. & S. Syst. 7, pt. 2:1731. 1830.

Loranthus marginatus Desr. in Lam. Encycl. 3:596. 1789.

A scandent shrub provided with aerial roots. Branches somewhat compressed and lenticellate-dotted. Leaves narrowly ovate or lance-ovate, conspicuously acuminate, rounded-obtuse at the base, firmly leathery, finely nervose on both surfaces, cartilaginous-margined, 7–12 cm. long, 3–5 cm. wide; petioles 5–10 mm. long. Ternations pedicelled. Racemes 1–3 in each axil, 3–8 cm. long. Bractlets persistent, connate. Flowers yellowish green, 3–4 mm. long. Fruit yellow or orange, 8–10 mm. long.

Widespread in Brazil. Costa Rica, Panama.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1287*. CHIRIQUÍ: Callejón Seco, Volcán de Chiriquí, *Woodson & Schery 486* and *504*; vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 808* and *932*; Río Chiriquí Viejo valley, Cerro Punta, *G. White 34*; Finca Lérida to Peña Blanca, *Woodson & Schery 292*; Boquete, *Davidson 859*; Bajo Chorro, Boquete, *Davidson 392, 908*.

3. STRUTHANTHUS ORBICULARIS (H. B. K.) Bl. in R. & S. Syst. 7, pt. 2:1731. 1830.

Loranthus orbicularis H.B.K. Nov. Gen. & Sp. 3:434. 1820.

Vines bearing adventitious roots, with long and flexuous branches, the branchlets twining, quadrate; the young leaves seem to serve as prehensile organs (they show petioles fully developed while the blades remain much smaller than the normal ones). Leaves broadly obovate to rounded, sometimes perfectly orbicular, coriaceous, rarely veiny, to 5 cm. long, 4 cm. wide; petioles 1–1.5 cm. long. Bractlets free, soon caducous. Ternations sessile. Flowers pedicelled, yellow or greenish yellow, 5–7 mm. long. Spikes solitary, rather stout (especially when fruiting), the rachis sharply angled, 7–15 cm. long. Fruit elliptic, purple to red-brown, about 1 cm. long.

Peru, Ecuador, Colombia. Rare in Brazil. Central America, where it is more widely dispersed.

BOCAS DEL TORO: Río Cricamola, *Woodson, Allen & Seibert 1908*; Chiriquí Lagoon, *von Wedel 2663, 1065*. CANAL ZONE: *White 121*; vicinity of Ancón, *Piper 6019*; Balboa, *Standley 29327*; Bellavista, *Macbride 2754*. COCLÉ: vicinity of El Valle, *Allen 1803*; *Seibert 417*; vicinity of Sta. Clara beach, *Woodson, Allen & Seibert 1700*. PANAMÁ: *Woodson, Allen & Seibert 1513*; Las Sabanas, *Standley 25936*; San José Island, *Johnston 518*; *Erlanson 73*; Saboga Island, *Miller 1938*. PROVINCE UNKNOWN: Quebrada de Oro, *Wheeler & Zetek 12-III-1923*.

4. STRUTHANTHUS ROTUNDATUS Rizz. in Rev. Brasil. Biol. 10 (4): 401. 1950.

Resembling S. *orbicularis* in habit. Branches terete, the branchlets compressed. Leaves perfectly elliptic or nearly rounded, slightly attenuate at the base, the apex emarginate and mucronate, moderately coriaceous, almost nerveless, 4–6 cm. long, 3–4.5 cm. wide; petioles 5–15 mm. long. Ternations pedicelled. Bractlets connate, persistent. Racemes solitary, 5–10 cm. long, the rachis compressed. Flowers deep yellow, about 7 mm. long. Fruit unknown.

Brazil, Panama.

Fig. 75. *Struthanthus rotundatus*; below: spike of *S. orbicularis*.

CHIRIQUÍ: Finca Lérida to Boquete, *Woodson, Allen & Seibert 1141*; vicinity of Cerro Punta, *Allen 1571*; pastures around El Boquete, *Pittier 2882*.

In general appearance, especially by its leaves, this species is very similar to S. *polyrhizus* Mart. too, but differs as follows: the former has racemes as long as the leaves or longer; the latter shows corymbs half as short as the leaves. So it may be understood why they have sometimes been confused.

The type (see figure in Rodriguesia, 18–19, tab. 8, 1956) conserved at the British Museum leaves no doubt as to the identity of Brazilian and Panamanian material.

6. PHTHIRUSA Mart.

PHTHIRUSA Mart. in Flora 13:110. 1830; Rizzini, in Dusenia 3 (6): 451. 1952.

Erect or scandent shrubs, the latter developing aerial roots. Leaves mostly leathery. Flowers often very tiny, tetra-hexamerous, in ternations; these in racemes, spikes, panicles or rarely subsolitary; bractlets connate. Stamens unequal, the filaments of the longer scalloped at both sides by pressure of the anthers of the shorter ones. Pollen grains of one type; triangular in shape, the exine finely granulose, showing three pores. Pistillate flowers with staminodia; staminate ones with vestigial style, this lacking stigma; androgynous flowers sometimes occur. Buds of the male flowers terete. Fruit baccate as in *Struthanthus*.

A genus of about 55 species, widely distributed throughout South America and the West Indies. It differs from the preceding by the combination of scalloped filaments, pollen grains of one type and terete male buds; thus, despite the opinion of Baehni and Macbride (Candollea 7:287–290. 1936–1938), it seems best to maintain it as a genus (see also Rodriguesia 18–19:87–234. 1956). The following are the only Central American species.

a. Leaves acute or acuminate. Inflorescence several together or branched. Flowers 4–6 mm. long.
  b. Flower clusters pedicellate, panicled.......... 1. P. ADUNCA
  bb. Flower clusters borne in spikes, sessile.......... 2. P. PITTIERI
aa. Leaves obtuse or nearly so. Inflorescences mostly solitary, unbranched. Flowers 1–2 mm. long.......... 3. P. PYRIFOLIA

1. PHTHIRUSA ADUNCA (Meyer) Maguire, in Bull. Torrey Bot. Club 75:301. 1948.

Loranthus aduncus Meyer, Prim. Fl. Esseq. 149. 1818.
Loranthus paniculatus H.B.K. Nov. Gen. & Sp. 3:422. 1820.
Loranthus conduplicatus H.B.K. loc. cit. 1820.
Loranthus magdalenae Cham. & Schl. in Linnaea 3:219. 1828.
Loranthus theobromae Willd. ex R. & S. Syst. 7:132. 1829.
Struthanthus aduncus (Meyer) G. Don, Gen. Syst. 3:414. 1834.
Phthirusa theobromae (Willd. ex R. & S.) Eichl. in Mart. Fl. Bras. 5, part 2:56. 1868.
Phthirusa paniculata (H.B.K.) Macbr. in Field Mus. Publ. Bot. 11:17. 1931.

Scandent shrubs bearing adventitious roots. Branches terete, the branchlets more or less compressed. Leaves ovate or oblong, rounded at the base, gradually acuminate, distinctly nervose, leathery, 4–7 cm. long, 2.5–4.5 cm. broad; petioles

1–2 cm. long. Flowers pale yellow, 4–6 cm. long, paniculate, the ternations pedicelled (pedicels 1–3 mm. long, rarely none); filaments provided with many glandules at the angles. Fruit oblong, pedicellate, orange, to 1 cm. long.

Brazil, where it is widely distributed, Peru, Venezuela (also very common there), Guianas, Paraguay, Panama. South American specimens are not different from Central American ones even in the least detail.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 2414*. CANAL ZONE: vicinity of Miraflores Lake, *G. White 158*; Bellavista, *Salvoza 1005*. CHIRIQUÍ: vicinity of Callejón Seco, Volcán de Chiriquí, *Woodson & Schery 500*. VERAGUAS: vicinity of Santiago, *Allen 1012*.

Ph. theobromae and *Ph. magdalenae* are not at all clearly distinct; as a matter of fact, examining the extremely rich South American material, numerous transitions are seen to occur from one to another. The other names above quoted are merely synonyms dealing with the priority question and deserve no more attention.

2. PHTHIRUSA PITTIERI Krause, in Fedde, Repert. Sp. Nov. 15 (1–3): 441. 1917.

Known only from original description which is, however, very complete. Branches terete. Leaves narrowly ovate or ovate-oblong, long-acuminate, rounded-obtuse at the base, 12–18 cm. long, 5–9 cm. broad. Ternations in axillary spikes, these numerous in each axil. Flowers 5 mm. long.

Endemic.

COLÓN: in the margins of Río Fató, *Pittier 3911*.

3. PHTHIRUSA PYRIFOLIA (H. B. K.) Eichl. in Mart. Fl. Bras. 5, pt. 2:36. 1868.

Loranthus pyrifolius H.B.K. Nov. Gen. & Sp. 3:441. 1820.

An erect shrub without aerial roots. Branches greatly flattened, the tips reddish-scurfy. Leaves ovate or elliptic, nearly rounded at the base, obtuse toward the apex, now and then mucronate or even caudate, distinctly veiny on both sides, to 10 cm. long, 5 cm. wide; petioles about 1 cm. long. Ternations perfectly sessile. Flowers very minute, 1–2 mm. long. Spikes axillary, solitary or 2 in each axil, unbranched, reddish-furfuraceous, 5–10 cm. long. Fruit oblong, 4–6 mm. long.

Panamanian specimens available agree exactly with Brazilian ones. Venezuela, Guianas, Colombia, Costa Rica, West Indies, etc.

CANAL ZONE: near Vigia and San Juan on Río Pequení, *Dodge, Steyermark & Allen 16571*; around Las Cruces, *Pittier 2623*; *Sutton Hayes 1022*; without locality, *Woodworth & Vestal 493*; Gatún Lake, *Bangham 441*; Changuinola Valley, *Dunlap 321*.

7. ORYCTANTHUS (Griseb.) Eichl.

ORYCTANTHUS Eichl. in Mart. Fl. Bras. 5, pt. 2:87. 1868.

Loranthus sect. *Oryctanthus* Griseb. Fl. Brit. West Ind. Isl. 311. 1860.

Erect shrubs, almost always with aerial roots starting from the base of the stem. Leaves opposite, coriaceous. Flowers minute, perfect, 6-merous, more or

Fig. 76. *Phthirusa pyrifolia*

less immersed in the rachis of the spikes; bractlets poorly developed or absent. Pollen grains strongly reticulate. Stigma capitate. Fruit baccate, the seeds albuminous.

About 18 species, uniformly distributed throughout the American tropics. The genus is noteworthy for its double-perianthed flowers sunk in the axis of the inflorescence.

a. Leaves sessile, cordate at the base.......... 1. O. CORDIFOLIUS
aa. Leaves petiolate, either rounded or acute at the base but not cordate.
b. Rachis glabrous, black. Bractlets with free margins. Flowers (buds and fruits) perpendicular to the rachis.......... 2. O. OCCIDENTALIS
bb. Rachis furfuraceous, more or less brown-reddish. Bractlets with the margins united with the rachis. Flowers (buds and fruits) oblique to the rachis.......... 3. O. SPICATUS

1. ORYCTANTHUS CORDIFOLIUS (Presl) Urban, in Engl. Bot. Jahrb. 24:348. 1897.

Viscum cordifolium Presl, Epim. Bot. 253. 1849.

A stout shrub with terete branches, the branchlets compressed, scarcely rusty-furfuraceous, becoming glabrate. Leaf blades sessile, broadly ovate, cordate at the rounded base, attenuate to the blunt apex, firmly coriaceous, nerves distinct but faint, about 7–12 cm. long, 4–8 cm. wide. Spikes axillary, solitary, to 8 cm. long, the peduncle 5–15 mm. long. Bractlets with free margins. Flowers or buds

deep red, 2 mm. long, inserted obliquely on the glabrous rachis. Fruit ovate, 5 mm. long.

Central America.

BOCAS DEL TORO: Isla Colón, *von Wedel 512*; vicinity of Nievecita, *Woodson, Allen & Seibert 1830*. CANAL ZONE: Quebrada Tranquila, *Dodge & Allen 17332*. COCLÉ: Penonomé, *Williams 196*. PANAMÁ: near Matías Hernández, *Standley 28923*.

2. ORYCTANTHUS OCCIDENTALIS (L.) Eichl. in Mart. Fl. Bras. 5, pt. 2:89. 1868.

Loranthus occidentalis L. Syst. ed. 10. 988. 1774.

Erect shrubs. Branches, terete, the branchlets slightly compressed, petioles (to 5 mm.. long) and peduncles (5–10 mm. long) rusty-furfuraceous, later subglabrate. Leaf blades very broadly ovate, almost orbicular at the base, scarcely constricted to the apex, this obtuse, thick and hard, nervation distinct or veinless, 3–10 cm. long, 2–8 cm. wide. Spikes solitary, to 3 cm. long; rachis glabrous. Bractlets with distinct margins. Flowers or buds becoming brown, 1–1.5 mm. long, perpendicular to the rachis. Fruit ovate, 4–5 mm. long, the apex not exceeded by the margin of the persistent calyculus.

West Indies, Costa Rica, Panama.

Fig. 77. *Oryctanthus spicatus*; below: spike of *O. occidentalis*.

CANAL ZONE: Juan Mina, *Piper 5703*; around Las Cruces, *Pittier 2622*; Las Cascadas Plantation, *Standley 25679*; Santa Rita Trail, *Cowell 74*; without locality, *Woodworth & Vestal 492*; Chagres, *Fendler 135*; Barro Colorado Island, *Shattuck 700.*

3. ORYCTANTHUS SPICATUS (Jacq.) Eichl. in Mart. Fl. Bras. 5, pt. 2:89. 1868.

Loranthus spicatus Jacq. Enum. Pl. Carib. 18. 1760.

An erect shrub 50–70 cm. tall. Branches terete, the slightly compressed tips, with petioles (1–5 mm. long) and rachis, reddish-scurfy but becoming more or less glabrous. Leaf blades ovate, sometimes orbicular-ovate, rounded at the base, moderately attenuate to the blunt apex, thickly leathery, lightly nerved (rarely nerveless), to 9 cm. long, 5 cm. broad. Spikes solitary, to 2 cm. long, stouter than in the preceding; peduncles to 5 mm. long. Bractlets not distinct from the rachis. Flowers or buds 1 mm. long, oblique to the rachis. Fruit ovate-oblong, about 5 mm. long, the apex evidently exceeded by the margin of the persistent calyculus.

West Indies, South and Central America.

CANAL ZONE: near Vigia and San Juan on Río Pequení, *Dodge, Steyermark & Allen 16577*; Ancón Hill, vicinity of Balboa, *Seibert 380, 410*; Barro Colorado Island, *Shattuck 590* and *Wilson 151*; Gatún Lake, *Wetmore & Abbe 148*; *Woodworth & Vestal 494.* CHIRIQUÍ: Gualaca, *Allen 5025.* COCLÉ: Penonomé, *Williams 195.* PANAMÁ: Tumba Muerto Road, *Standley 29831*; near Punta Paitilla, *Standley 26249.*

The morphological facts by which O. *occidentalis* differs from O. *spicatus* are minute and tedious ones. Notwithstanding, and worth noting, additional characters may be found in the spikes: in the first species these are slender, blackish and supported by a peduncle longer than 5 mm.; in the second, the spikes are stouter, reddish-brown and short-peduncled or even sessile.

8. DENDROPHTHORA Eichl.

DENDROPHTHORA Eichl. in Mart. Fl. Bras. 5, pt. 2:102. 1868; Urban, in Engl. Bot. Jahrb. 24:370. 1897.

Erect shrubs, more or less yellow, lacking adventitious roots. Leaves opposite, small or wanting. Cataphylls poorly developed. Flowers trimerous, very minute, dioecious, deeply immersed in depressions in the rachis of the spikes. Anther cells confluent, dehiscing transversely; pollen grains globose, the exine smooth. Pistillate flowers without staminodia. Staminate flowers showing no style. Fruit a berry, the seeds with endosperm.

A genus of about 32 species, thriving better in high-altitudinal places, chiefly in South America and the West Indies. It is very similar in appearance to *Phoradendron,* from which may be distinguished as indicated in the above key, except that its species are less robust with leaves small or reduced to scales.

a. Developing normal leaves .... 1. D. COSTARICENSIS
aa. Leaves wanting or reduced to scales .... 2. D. BISERRULA

1. Dendrophthora costaricensis Urban, in Ber. Deutsch. Bot. Gesell. 14:285. 1896.

An erect shrub. Branches terete, the branchlets somewhat compressed, striate-rugose. Leaves obovate-spatulate, long-attenuate to the base, the apex rounded and emarginate, veinless, moderately coriaceous, 2–3 cm. long, 1–1.5 cm. broad; petioles about 5 mm. long. Spikes solitary, axillary, 1–2-jointed, 5–15 mm. long, the peduncles 0–3 mm. long. Flowers 6-seriate, 18–40 in each joint. Fruit white, globose.

Costa Rica, Panama.

chiriquí: Bajo Chorro, Boquete, *Davidson 369*; upper belt of Chiriquí Volcán, *Pittier 3100*.

2. Dendrophthora biserrula Eichl. in Mart. Fl. Bras. 5, pt. 2:104. 1868.

An upright, densely branched undershrub attaining 25 cm. in height, the branches terete. Leafless. Scales about 1 mm. long. Spikes very numerous, axillary, solitary, 1-articulate, to 2.5 cm. long with 4–24 flowers, these 2-seriate; the peduncles 5–8 mm. long; the rachis quadrate. Fruit globose, white.

Central America.

chiriquí: Volcán de Chiriquí, Boquete, *Terry 1333*, *Maxon 5374a*; around El Potrero, *Pittier 3073*.

This species is remarkable by supporting usually a vigorous growth of filamentous as well as foliaceous lichens, which give it a peculiar appearance.

Fig. 78. *Dendrophthora biserrula*

9. PHORADENDRON Nutt.

Phoradendron Nutt. in Journ. Acad. Philadelphia ser. 2. 1:185. 1847; Trelease, The Genus Phoradendron (Urbana, Ills.: The University of Illinois, 1916).

Erect and rootless shrubs. Leaves opposite, rarely reduced to scales. Flowers as in *Dendrophthora*, except that they are arranged in definite rows on the spike

joints (2 or 3 series over each side of the joints). Anthers 2-celled, dehiscing by longitudinal slits; pollen grains globose, the exine smooth. Fruit as in the preceding genus.

The New World mistletoe includes about 300 species. In the Old World it is replaced by *Viscum*.

a. Cataphylls present on all internodes of the branches.
b. Branches cymosely or dichotomously forking at every node.
c. Shoots obviously swollen below the nodes. Leaves rounded at the apex. Fruit globose, with erect tepals .... 1. P. PERGRANULATUM
cc. Shoots not enlarged below the nodes. Leaves, at least the upper of them, acute. Fruit elongated, with connivent tepals .... 2. P. ROBALOENSE
bb. Branches not forking at all nodes.
c. Basal scales of the spikes forming a large and deep funnel-shaped tube enclosing the peduncle .... 3. P. SUPRAVENULOSUM
cc. Scales not forming a tube, thus the peduncle free.
d. Leaves to 3 cm. broad, basinerved. Cataphylls 2–4 pairs on all joints .... 4. P. WOODSONII
dd. Leaves mostly broader, nerveless or obscurely pinnately nerved. Cataphylls a single pair on all joints, usually 2–5 pairs on the lowermost .... 5. P. PIPEROIDES
aa. Cataphylls present only on the lowest internode of each branch.
b. Branches terete. Spikes typically 2-jointed.
c. Spike joints slender, up to 20-flowered in 4 series .... 6. P. CRISPUM
cc. Spike joints rather stout, the more numerous flowers in 6 series .... 7. P. ALLENII
bb. Branches 4-angled or flattened. Spikes mostly 3-(or more) articulate.
c. Shoots prevailingly flattened or 2-edged.
d. Branchlets subquadrangulate toward the tip .... 8. P. SEIBERTII
dd. Branchlets of the same shape as the branches.
e. Leaves up to 1.5 cm. wide. Spike joints clavate or turbinate, stout.
f. Cataphylls two pairs above the base. Joints clavate, 4–8-flowered. Leaves to 7 cm. long .... 9. P. CORYNARTHRON
ff. Cataphylls one pair, strictly basal. Joints turbinate, 16–24-flowered when pistillate (staminate ones to 70-flowered). Leaves 8–15 cm. long.
g. Flowers 6-ranked, 30–70 in each joint when staminate .... 10. P. NOVAE-HELVETIAE
gg. Flowers 4-ranked, about 30 in each joint when staminate. 11. P. TONDUZII
ee. Leaves 1.5–4 cm. wide. Spike joints terete.
f. Spikes with 7–10 slender joints. Leaves 2.5–4 cm. broad .... 12. P. GRACILISPICUM
ff. Spikes with 5–7 rather stout joints. Leaves up to 3 cm. broad.
g. Leaves typically undulate or even crisped .... 13. P. UNDULATUM
gg. Leaves entire .... 14. P. COOPERI
cc. Branches typically 4-sided or 4-lined.
d. Leaves obovate, most of them emarginate. Spike joints 4–6-flowered. Fruit tuberculate .... 15. P. MUCRONATUM
dd. Leaves oblong, oblong-lanceolate or oblong-obovate. Spike joints 8–20-flowered. Fruit smooth.
e. Leaves obovate-oblong. Fruit with upright tepals. Joints 6–8-flowered .... 16. P. TRINERVIUM
ee. Leaves lance-oblong or oblong. Fruit tepals closely connivent. Joints 14–20-flowered .... 17. P. VENEZUELENSE

1. PHORADENDRON PERGRANULATUM Trel. in Ann. Missouri Bot. Gard. 27:308. 1940.

A stout shrub cymosely branching at every node; shoots terete, much dilated and somewhat compressed below the nodes. Cataphylls a single basal pair on all joints, the margin almost fimbriate. Leaves falcately oblong, attenuate to both ends, rounded at the apex, acute at the base, nerveless, coriaceous, drying somewhat

crisped marginally, 5–9 cm. long, 1.5–3 cm. wide; petioles scarcely 2–4 mm. long. Spikes solitary, mostly 4-articulate, about 3 cm. long; peduncle 3–5 mm. long; joints slender, 5–8 mm. long, 4–8-flowered in 4 series. Fruit rounded, varnished, the tepals erect, about 3 mm. in diameter.

Endemic.

COCLÉ: vicinity of El Valle, *Allen 777.*

2. PHORADENDRON **robaloense** Woods., n. sp. Nomen tantum in sched.

Inter affines (praesertim *P. henslovii* Robs.) haec species distinctissima et statim discernenda vaginis cataphyllaribus in tubum amplum 3–10 mm. longum connatis, foliis spicisque neglectis.

Fruticulus dioicus circa 2.5 m. altus, ramis dichotomis teretibus; internodiis 4–8 cm. longis. Vagina cataphyllaris 3–10 mm. longa, tubulosa, in dentes 2 latos rotundatos divisa. Folia obliqua, ovato-lanceolata, basi vel obtusa vel cuneata, apicem versus longe attenuata, imo apice ex indole cuta, crasse coriacea, siccitate marginibus undulata, obsolete palmatinervia aut avenia, 8–12 cm. longa, 2–4.5 cm. lata; petiolis crassis, circa 1 cm. longis. Spicae 2–3-nae in axillis, graciles, 3–4-articulatae, 3–5 cm. longae; pedunculis 8 mm. longis; articulis plus minusve 1 cm. longis, 4-seriatim 6–14-floris; floribus femineis. Baccae elongatae, perigonio clauso coronatae, 5–6 mm. longae.

CHIRIQUÍ: Bajo Mona, Robalo Trail, alt. 1500–2100 m. s. m., *Paul H. Allen 4838* (MO, HOLOTYPE).

Ph. robaloense Woods. ex Rizz. is a very striking species and is easily distinguished from its allies (*Aequatoriales Cymosae*) by the tubular cataphylls, the few-flowered spike joints and the elongated fruits.

3. PHORADENDRON SUPRAVENULOSUM Trel. Genus Phoradendron. 154. 1916.

Branches inconspicuously angled, compressed and enlarged below the nodes; internodes rather long (4–7 cm.). Cataphylls a single pair at each joint, 1–2 cm. above the base, parted, 2 mm. high. Leaves oblong, moderately falcate, very acuminately pointed, cuneate to the base, moderately coriaceous, obscurely 5-nerved, to 13 cm. long, 6 cm. broad; petioles about 1 cm. long. Spikes solitary, 3–5-articulate, 4–7 cm. long; peduncle 5–7 mm. long, enclosed within a large, funnel-shaped tube formed by the basal scales; joints rather stout, to 2 cm. long, 30–50-flowered, the flowers in 6 series. Fruit apparently elongated, with connivent tepals.

Previously known from Guatemala, Nicaragua and Costa Rica.

DARIÉN: Crist, Cana-Cuasi Trail, *Terry 1571.*

This specimen, insufficient for a complete study, differs from *Ph. supravenulosum,* as described by Trelease, in some small details and approaches *Ph. membranaceum* in certain others. Future studies may perhaps determine segregation as a proper species.

Fig. 79. *Phoradendron robaloense*

4. PHORADENDRON WOODSONII Trel. in Ann. Missouri Bot. Gard. 27:308. 1940.

Branches slender, terete, regularly forked. Cataphylls a basal pair followed by 2 or 3 others, bifid at all internodes. Leaves ovate-oblong, scarcely cuneate to the rounded base, more or less abruptly acuminate, moderately leathery, obscurely 3–5-nerved, thickly cartilagineous-margined, 5–7 cm. long, 2–3 cm. wide; petioles nearly lacking. Spikes solitary, 5–6-articulate, 3–5 cm. long; peduncle 3–5 mm. long; joints lightly clavate, 5–8 mm. long, with about 10 flowers in 4 ranks. Fruits subglobose, 4 mm. long, the tepals inflexed.

Endemic.

COCLÉ: between Las Margaritas and El Valle, *Woodson, Allen & Seibert 1302* (type).

5. PHORADENDRON PIPEROIDES (H. B. K.) Nutt. in Journ. Acad. Nat. Sc. Philadelphia, ser. 2, 1:185. 1847.

Viscum latifolium Sw. Fl. Ind. Occ. 1:268. 1797, non Lam.
Loranthus piperoides H.B.K. Nov. Gen. & Sp. 3:443. 1820.
Phoradendron latifolium (Sw.) Griseb., Fl. Brit. West Ind. Isl. 314. 1860.

A very variable shrub, abundantly branched. Shoots slender, slightly compressed above, soon becoming terete. Cataphylls a single pair on every joint, 2–5 pairs on the lowest one, pointed. Leaves, at least most of them, obliquely broadly ovate, angustate both toward the base and apex, acuminate, coriaceous, marginally crisped and brown to black in drying, nerveless or obscurely pinnately veined beneath, 5–12 cm. long, 2.5–4.5 cm. broad; petioles about 5 mm. long. Spikes clustered, slender, mostly 6-jointed, 4 cm. long; peduncle nearly suppressed; joints terete, 5 mm. long, 6–20-flowered, the flowers 4-ranked. Fruits subglobose, yellow, 4 mm. in diameter, with connivent tepals.

Widely distributed through the New World.

BOCAS DEL TORO: vicinity of Nievecita, *Woodson, Allen & Seibert 1843*; Río Cricamola, between Finca St. Louis and Konkintoe, *Woodson, Allen & Seibert 1900, 1904*; Almirante, *Cooper 93, 193*. CANAL ZONE: Chagres, *Fendler 136*; Barro Colorado Island, *Shattuck 1138*; Fuertes House, *Woodworth & Vestal 663*; Mindí, *Sutton Hayes 616*. CHIRIQUÍ: El Boquete, *Pittier 3345*; around Caldera, *Pittier 3357*; Bajo Mona, *Davidson 522*. COCLÉ: above Penonomé, *Williams 258*. DARIÉN: Chepigana, Cana-Cuasi Trail, *Davidson & Terry 1572*. PANAMÁ: Sabanas Road, *Gillespie P-40*.

6. PHORADENDRON CRISPUM Trel. Genus Phoradendron 77. 1916.

A moderately branched undershrub 30–60 cm. tall, the branches terete. Cataphylls a single basal pair, short. Leaves obovate to round-obovate, a little attenuate to the base, firmly membranaceous, veinless or very obscurely 3-nerved, drying crisped, 3.5–5 cm. long, 1.5–3 cm. wide; petioles 4–6 mm. long. Spikes solitary, with 2–3 short articles, 5–15 mm. long; peduncle almost suppressed; joints 10–20-flowered in 4 series. Fruits white, translucent.

Panama and Costa Rica.

CHIRIQUÍ: Boquete, Volcán de Chiriquí, *Davidson 992*.

7. PHORADENDRON ALLENII Trel. in Ann. Missouri Bot. Gard. 27:307. 1940.

Very similar to *Ph. crispum* Trel., but the flowers are constantly more numerous and 6-ranked. Branches terete. Cataphylls only a basal pair on the lowermost internode of the shoots. Leaves obovate, to 6 cm. long, 2.5 cm. broad, finely 3-nerved; petioles about 5 mm. long. Spikes solitary, stout, 2–3-articulate, to 2 cm. long; peduncle about 4 mm. long; joints 5–8 mm. long, 20–40-flowered irregularly arranged in 6 rows. Fruits globose, 4–5 mm. in diameter, the tepals more or less erect.

Endemic.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 792* (type).

8. PHORADENDRON **seibertii** (Trel.) Rizz., nov. stat.

Phoradendron corynarthron Eichl. var. *seibertii* Trel. in Ann. Missouri Bot. Gard. 24:187. 1937.

Branches 2-edged, the branchlets more or less 4-angled. Cataphylls a single basal pair, tubular, the margin parted. Leaves narrowly oblong, some of them almost spatulate, rounded at the apex, attenuate to the base, nerveless, coriaceous, 4–7 cm. long, 1–1.5 cm. wide; petioles to 4 mm. long. Spikes solitary, slender, 4–6-articulate, to 2 cm. long; peduncle about 2 mm. long; joints short, terete, 10–18-flowered, the flowers in 4 rows.

Endemic.

COCLÉ: El Valle de Antón, *Seibert 411* (type).

Ph. corynarthron Eichl. always shows clavate spike joints with 4 to 8 flowers, flattened branchlets and subacute leaves, thus being clearly different from *Ph. seibertii* (Trel.) Rizz.

9. PHORADENDRON CORYNARTHRON Eichl. in Mart. Fl. Bras. 5, pt. 2:115. 1868.

Phoradendron davidsoniae Standl., Field Mus. Publ. Bot. 22:17. 1940.

A handsome yellow (drying yellowish-brown) undershrub with flattened branches, the branchlets somewhat enlarged below the nodes. Cataphylls usually two pairs, one about 0.5–1 cm. above the node and the other 1.5–2 cm. above the first, pointed. Leaves lanceolate to narrowly oblong, rarely falcate, attenuate to both ends, subacute at the apex, cuneate to the base, moderately coriaceous, more or less revolute along the margins in drying, nearly nerveless to finely 3-nerved, 4–7 cm. long, 0.8–1.5 cm. wide; petioles about 5 mm. long. Spikes solitary, typically 3-articulate, 1–1.5 cm. long (becoming 2–3.5 cm. when fruiting); peduncle 1–5 mm. long; joints clavately 4–8-flowered in 4 series, 2–10 mm. long. Fruit round, white, 3 mm. in diameter, the tepals closely connivent.

Central America, widely dispersed in Panama.

CHIRIQUÍ: vicinity of Finca Lérida, *Woodson & Schery 220*; Bajo Mona, mouth of Quebrada Chiquero along Río Caldera, *Woodson & Schery 294*; Loma Sardina, *Allen 4769*; vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 929*; Boquete, *Davidson 740* (type of *Phoradendron davidsoniae* Standl.) and *923*. COCLÉ: Aguadulce, in savannas, *Pittier 4955*.

Ph. corynarthron must not be confused with *Ph. rigidum* Urban, from Venezuela. This shows shorter spikes bearing 2–3 joints, which are 10-flowered, and broader leaves.

10. Phoradendron novae-helvetiae Trel. in Ann. Missouri Bot. Gard. 27:307. 1940.

A dioecious, very bushy shrub up to 4.5 m. tall. Branches rather stout, 2-edged, the branchlets highly compressed. Cataphylls a single pair, strictly basal, large, up to 3 mm. long. Leaves obliquely lanceolate, very acute, cuneately long-attenuate to the base, thus almost sessile or subpetioled for about 1 cm., finely 3–5-nerved, somewhat coriaceous, to 15 cm. long, 1.5 cm. broad. Spikes both solitary and clustered, 3–4-articulate, turbinate, the flowers 6-ranked; pistillate ones much stouter, to 4 cm. long, the joints 1 cm. long, 16–24-flowered; staminate spikes slender, to 6 cm. long, the joints 6–12 mm. long, 30–70-flowered; peduncle in any case 2–3 mm. long. Fruits globose, the tepals closely inflexed.

Endemic.

chiriquí: vicinity of Finca Lérida, *Allen 4752*; vicinity of New Switzerland, *Allen 1399* (type); Cerro Vaca, *Pittier 5376*.

Ph. novae-helvetiae, a pretty species, is very similar to *Ph. tonduzii* Trel., reported to occur in Panama (see below); it may be distinguished by the 6-seriate flowers and 30–70-flowered male joints (instead of 4-ranked as Trelease says).

11. Phoradendron tonduzii Trel. Genus Phoradendron 67. 1916.

Authoritatively (see Standley's Flora of Costa Rica, p. 406) but not unquestionably Panamanian; however, it may be expected.

In habit of foliage and inflorescence it is closely related to *Ph. novae-helvetiae* Trel., above described. They are readily distinguishable by the flower disposition and by the number of male flowers.

12. Phoradendron gracilispicum Trel. Genus Phoradendron 130. 1916.

Trelease mentions a collection from Chiriquí. The following description is taken from the original (*ibidem*):

Branches ancipital and rather persistently 2-keeled, the internodes 4–6 cm. long. Cataphylls only basal or followed by a second pair some 2 cm. higher. Leaves lanceolate or oblong-acute, the base cuneate, devoid of nerves, 10–16 cm. long, 2.5–4 cm. broad; petioles about 1 cm. long. Spikes often clustered, markedly slender, very long (to 7 cm.), reddish, showing about 10 thin joints some 12-flowered in 4 (6) series; peduncle 2 mm. long, often followed by 1 or 2 partly or wholly sterile joints, the scales ciliolate. Young fruit elongated, the tepals connivent.

13. Phoradendron undulatum (Pohl) Eichl. in Mart. Fl. Bras. 5, pt. 2:122. 1868.

Viscum undulatum Pohl, in DC. Prodr. 4:282. 1830.

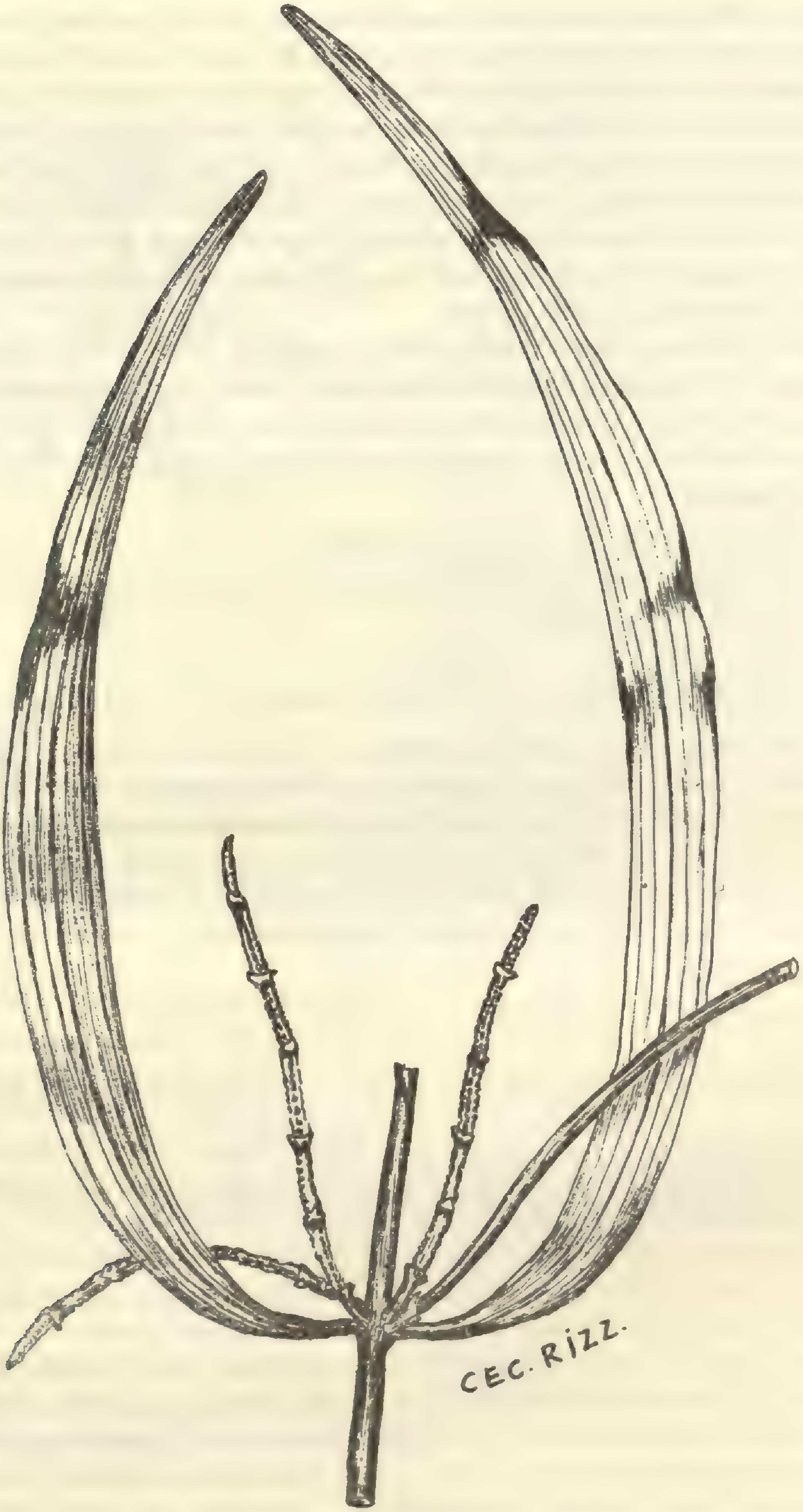

Fig. 80. *Phoradendron novae-helvetiae*

Yellow, with a brownish tint, moderately tall shrub hanging from trees. Branches ancipital and 2-keeled, especially toward the tips. Cataphylls a nearly basal pair followed by 2–3 additional ones, rather pointed. Leaves lanceolate, not rarely somewhat ovate, acuminate, under lens rugose, the nerves wanting, the margins callose-thickened and conspicuously undulate, 7–12 cm. long, 2–4 cm. wide; petioles 3–8 mm. in length, canaliculate above. Spikes many times clustered, 2–5 cm. long, with 5–9 moderate joints; peduncle none or up to 8 mm. long; joints mostly 10-flowered in 2 ranks, 2–5 mm. long. Fruits round-ovoid, smooth, 3 mm. in diameter, the tepals slightly parted.

Another interesting finding of a plant, previously known only from Brazil, in Panama. The excellent specimen, mentioned below, minutely examined and compared with several Brazilian ones, agrees even in the smallest details as, for instance, in the callose-margined and finely verrucose leaves.

Brazil, Panama.

CHIRIQUÍ: pastures around El Boquete, *Pittier 2932.*

Ph. gracilispicum Trel. is to be distinguished from the above by it longer, slender and many-jointed spikes.

14. PHORADENDRON COOPERI Trel. Genus Phoradendron 67. 1916.

Branches rather stout, 2-sided or ancipital. Cataphylls a single, strictly basal pair, pointed. Leaves falcately lanceolate to oblong-lanceolate, long-attenuate to the somewhat obtuse apex, thin, finely 5-nerved, cuneately subpetioled for 1–1.5 cm., to 20 cm. long, 2.5 cm. broad. Spikes solitary, 3–4-articulate, about 3–4 cm. long; peduncle nearly supressed; joints 16–25-flowered in 4 ranks, 8–10 mm. long. Fruits round, 3 mm. in diameter, the tepals closely meeting.

Central America.

CHIRIQUÍ: Boquete, *Davidson 580.*

15. PHORADENDRON MUCRONATUM (DC.) Kr. et Urb. in Engl. Bot. Jahrb. 24: 352.

Viscum mucronatum DC. Prodr. 4:282. 1830.
Phoradendron emarginatum Mart. ex Eichl., in Mart. Fl. Bras. 5, pt. 2:118. 1868.
Phoradendron emarginatum var. *minor* Eichl. loc. cit. 119. 1868.
Phoradendron minor (Eichl.) Trel., The Genus Phoradendron 117. 1916.

Branches somewhat nodose, the branchlets sharply 4-angled. Cataphylls a single basal pair, 2 mm. long. Leaves obovate, often emarginate, cuneate to the base, coriaceous, distinctly 3–5-nerved, to 3.5 cm. long, 2 cm. broad; petioles about 2–4 mm. long. Spikes solitary, subsessile, 3–4-jointed, 5 mm. long, when fruiting to 1.5 cm. long; joints 4–6-flowered in 4 series. Fruits ovoid, tuberculate, 3–4 mm. long, the tepals nearly erect.

South and Central America, West Indies.

PANAMÁ: swamp between El Jagua Hunting Club on Río Jagua and El Congor Hill, *Hunter & Allen 474.* COCLÉ: Aguadulce, *Pittier 4956.*

Fig. 81. *Phoradendron mucronatum*

As shown by Urban, *Ph. emarginatum* (Brazil) only differs from *Ph. mucronatum* (West Indies) by the larger leaves and longer spikes. The var. *minor* of the former species, with smaller leaves and shorter spikes, is intermediate between the two. Actually, there are no clear-cut differences.

Southern Brazilian specimens are constantly stouter than Central American and West Indian ones; but the northeastern Brazilian material is smaller than the former and approaches the latter.

In short: *Ph. mucronatum* is a South and Central American and West Indian rather variable entity, well characterized and easily recognizable by the obovate-emarginate leaves, 4-angled branches, 4–6-flowered spike joints and verrucose fruit—as it is evident from the examination of exceedingly abundant herbarium material.

16. PHORADENDRON TRINERVIUM Griseb. Fl. Brit. West Ind. Isl. 314. 1860.

Phoradendron rubrum var. *brevispica* Eichl. and var. *latifolia* Eichl. in Mart. Fl. Bras. 5, pt. 2:121. 1868.

Branches toward the tips rhombically quadrangulate, the branchlets somewhat compressed and swollen below the nodes. Cataphylls a single basal pair, short. Leaves narrowly obovate or elliptical-obovate, angustate to the base, very obtuse, almost nerveless despite the specific name, coriaceous, 2–5 cm. long, 1–1.5 cm. wide; petioles 2–4 mm. long. Spikes solitary or clustered, 3–4-articulate, up to 3 cm. long; peduncle 1–2 mm. long; joints slender, 10–18-flowered in 4 series, 4–7 mm. long. Fruit yellow, ovate, 3–5 mm. long, the tepals erect, parted.

West Indies, Panama.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 2763*.

17. PHORADENDRON VENEZUELENSE Trel. Genus Philodendron 111. 1916.

Phoradendron herrerense Trel. in Ann. Missouri Bot. Gard. 27:307. 1940.
Phoradendron sonanum Trel. loc. cit. 308. 1940.

A rather variable, androgynous shrub. Branches 4-lined, the branchlets quadrangulate, slightly compressed and somewhat enlarged below the nodes. Cataphylls a single basal pair, parted. Leaves lance-oblong, more or less falcate, obtuse or subacute, sometimes shortly mucronate, attenuate to the base, leathery, indistinctly

Fig. 82. *Phoradendron venezuelense*

3–5-nerved or nearly nerveless, cartilaginous-margined, 3–6 cm. long, rarely up to 8 cm., 7–15 mm. broad; petioles 2–5 mm. long. Spikes mostly clustered, slender, often 3-articulate (seldom to 5-jointed), about 1.5 cm. long, but attaining to 5 cm. when fully developed; peduncle 3–10 mm. long; joints 10–24-flowered, the flowers 4-seriate, to 1 cm. long. Fruit globose, yellow, 3 mm. in diameter, the tepals closely connivent.

Widely distributed both in Venezuela and Panama. Also in Colombia and the West Indies, where it is rare.

BOCAS DEL TORO: Water Valley, *von Wedel 936*; Chiriquí Lagoon, *von Wedel 1578, 2518, 2599, 2648*. CANAL ZONE: Ancón Hill, vicinity of Balboa, *Seibert 408*; around Gamboa, *Pittier 2604*; Barro Colorado Island, near Barbour Point, *Wilson 146*. HERRERA: Pesé, *Allen 798* (type of *Ph. herrerense* Trel.). PANAMÁ: Sabanas near Chepo, *Hunter & Allen 78*; on Sabanas, road to Chepo, *Hunter & Steyermark s. n.*; Río Tecumen, *Standley 26552*; along Corozal Road, *Standley 26869*; Llanos de Panamá Viejo, *Heriberto 288*. VERAGUAS: hills of Soná, *Allen 1033* (type of *Ph. sonanum* Trel.). PROVINCE UNKNOWN: *Sutton Hayes 829*.

Ph. herrerense Trel. only differs from *Ph. venezuelense* in the more regularly branched stem; *Ph. sonanum* Trel. is distinguished from the latter by some longer, 3–5-jointed spikes; in both cases the differences are too poorly developed to be taken into account.

OPILIACEAE

By LORIN I. NEVLING, Jr.

1. AGONANDRA Miers

Agonandra Miers, in Ann. Nat. Hist. ser. 2. 8:172. 1851, nomen; Benth. & Hook. f. Gen. 1:349. 1862.

Dioecious trees, the bark generally corky. Leaves alternate, simple, thin, usually small, ovate to elliptic, petiolate. Inflorescences axillary, racemose, bracteate. Flowers small, green, pedicellate. Calyx small, usually crateriform, (5- or) 4-lobed or undulate. Petals 4 (or 5), free, valvate, especially caducous in pistillate flowers. Stamens 4 (or 5), antipetalous, the filaments filiform, the anthers ovoid; absent in pistillate flowers. Disc annular or cupuliform, irregularly lobed, more or less connate at the base, generally erect. Pistil 1, superior, the ovary 1-loculate, the style generally obsolete, the stigma 4-lobed. Fruit a berry.

In the past pistillate flowers of this genus have been characterized by the absence of petals. Examination of the single collection from Panama clearly shows the presence of petals and also reveals their caducous nature.

Approximately a dozen species distributed from Mexico to Argentina. Known from a single species in Panama.

Fig. 83. *Agonandra brasiliensis*

1. Agonandra brasiliensis Benth. & Hook. f. Gen. 1:349. 1862.

Trees to 8 m. tall, the bark rough, brown, the branchlets slender, terete, glabrous, olive-green. Leaves ovate, 2.5–5.5 cm. long, 2–3 cm. broad, abruptly and briefly acuminate at the apex, obtuse and atenuate at the base, glabrous, the costa plane to immersed above, emersed below, the primary lateral veins prominulous; petiole 3–9 mm. long. Staminate inflorescence 30- to 75-flowered, farinose, the rhachis 3–7 cm. long. Staminate flowers (immature): pedicel about 0.5 mm. long; calyx crateriform, about 0.5 mm. long, farinose, undulate; petals 5, ovate, about 1.5 mm. long, 0.75 mm. broad, farinose without, glabrous within; stamens 5, the filaments 1–2 mm. long, glabrous, the anthers about 0.5 mm. long and broad; disc 5-lobed, the lobes very nearly free, about 0.5 mm. long, fleshy, truncate, obscurely and irregularly lobed at the apex, glabrous; pistillode conical, about 0.75 mm. long, glabrous. Pistillate inflorescences 10- to 15-flowered, farinose, the rhachis 0.5–4.5 cm. long. Pistillate flowers: pedicel 0.5–0.75 mm. long; calyx crateriform, about 0.25 mm. long, farinose without, the margin undulate; petals 4, ovate-trigonal, about 1 mm. long, 0.5 mm. broad at the base, farinose without, indefinitely papillate to glabrous within; disc annular, about 0.25 mm. tall, irregularly lobed to the middle, glabrous; ovary doleiform, 0.5–0.75 mm. long, glabrous, the style obsolete, the stigma 4-lobed. Berry ovoid, 12–15 mm. long, 10–12 mm. in diameter, glabrous; pedicel 5–8 mm. long.

Central and South America. The single collection examined was flowering and fruiting in February–March and was collected at an altitude of 50–1000 ft.

COCLÉ: Penonomé and vicinity, *R. S. Williams 368.*

OLACACEAE

By LORIN I. NEVLING, Jr.

Armed or unarmed trees, shrubs or perhaps vines, autotrophic or reportedly hemiparasitic. Leaves alternate, sometimes opposite, simple, generally entire, pinnately veined, petiolate; estipulate. Inflorescences axillary, panicles, racemes, cymes or umbels, often fasciculate. Flowers dichlamydeous, bisexual or rarely polygamodioecious, sometimes polymorphic, actinomorphic, generally small and inconspicuous. Calyx small, gamosepalous, crateriform to campanulate, usually with a 3- to 6-toothed margin, free or basally adnate to the ovary or to the disc, sometimes accrescent. Petals 3–6, usually the same number as calyx lobes, free or connate, valvate or imbricate in bud. Disc sometimes present, simple or cupuliform. Stamens generally the same number as, or twice the number of, petals, the anthers dehiscing longitudinally or by valves. Pistil 1, the ovary superior or rarely half-inferior, sessile, generally 2- to 5-loculate, the ovules the same number as locules, pendulous, integuments 0, 1 or 2, the style simple, sometimes heteromorphic, terminal, elongate to obsolete, the stigma often 3-parted. Fruit mostly a drupe, sometimes accompanied by a colorful accrescent calyx.

A pantropic family of about 25 genera and 300 species. Four genera are known from Panama. A fifth genus, *Chaunochiton,* is known from Costa Rica, Guiana and northern Brazil. Whether this disjunction is real or is an artifact of collection is not known at this time.

a. Calyx crateriform or cupuliform, free from the ovary, with 3 to 6 lobes or teeth; ovary superior; ovules with 1 or 2 integuments; fruit a drupe; plants root parasites (*Ximenia*) or autotrophes.
  b. Petals 5–6, free or connate, glabrous to more or less villous within; stamens 5–6 or 10–12; stigma 3- to 5-lobed; unarmed autotrophic shrubs or trees; leaves and bark with either resin canals or laticiferous ducts or both.
    c. Leaves and bark with resin canals and laticiferous ducts; pubescence branched; calyx with 5–6 teeth, not accrescent; petals connate; ovary 3- or 4-loculate (by abortion from 5) .... 1. MINQUARTIA
    cc. Leaves and bark with laticiferous ducts but lacking resin canals; pubescence unbranched; calyx with 5–6 teeth or lobes, accrescent; petals free; ovary with 3 locules .... 2. HEISTERIA
  bb. Petals 4–5, free, densely set with barbed hairs within; stamens 8–10; stigma minutely capitate; parasitic shrubs or trees, armed with axillary spines; leaves and bark lacking laticiferous ducts and resin canals .... 3. XIMENIA
aa. Calyx reduced, adnate to the ovary; ovary half-inferior; ovules lacking integument; spurious fruit drupaceous (eccentrically annulate at the apex); plants unarmed root parasites .... 4. SCHOEPFIA

1. MINQUARTIA Aubl.

MINQUARTIA Aubl. Hist. Pl. Guyan. Franç. Suppl. 4. *t. 370.* 1775.

Secretania Mull.-Arg. in DC. Prod. 15^2:227. 1866.
Minguartia Miers, in Journ. Linn. Soc. 17:338. 1879.

Unarmed autotrophic trees, the young branches generally densely rusty-tomentulose, the hairs branched, the older stems often perforated. Leaves alternate,

elliptic, acuminate at the apex, glabrous above, glabrescent below, with resin canals and laticiferous ducts. Inflorescences spicate, bracteate. Flowers bisexual, hypogynous, small. Calyx cupuliform to crateriform, small, (6-) 5-toothed, persistent but not accrescent. Petals 5 (or 6), connate into a campanulate corolla tube, puberulent to villous within, the lobes valvate in bud. Stamens 10 (or 12), in two whorls, the anthers dehiscing longitudinally, the filaments filiform, adnate to the corolla tube, antipetalous generally longer. Ovary 5-merous but often reduced to 3 or 4 locules by abortion, the stigma 3- to 5-lobed. Fruit a small ovoid or round drupe.

Three or four species distributed in Panama, Ecuador, Guiana and Brazil. A single species is known from Panama.

1. Minquartia guianensis Aubl. Hist. Pl. Guyan. Franç. Suppl. 4. *t. 370.* 1775.

Secretania loranthacea Mull.-Arg. in DC. Prod. 15^2:227. 1866.

Trees to 30 m. tall, the young branches angular, glabrous. Leaves elliptic, 8–16 cm. long, 3.0–7.5 cm. broad, abruptly and briefly acuminate at the apex, rounded or obtuse at the base, chartaceous, glabrous, the costa emersed above and below, the primary lateral nerves numerous, conspicuous; petiole 5–23 mm. long, broadly canaliculate. Inflorescence spicate, rusty-tomentulose, the rhachis elongating to 5 cm. long, the flowers sessile, subtended by small ovate bracts. Calyx cupuliform, about 1 mm. long, 1.5–2.0 mm. in diameter, 5-toothed, rusty-tomentulose without; petals 5, connate into a campanulate corolla tube, the tube 1.0–1.5 mm. long, tomentulose without, black-punctate within, the lobes 1.0–1.5 mm. long, 1 mm. broad, villous within; stamens 10, inserted just below the orifice, the alternipetalous inserted slightly lower than the antipetalous, the anthers broader than long, minute, the filaments about 0.5 mm. long, glabrous; ovary globose, about 1.5 mm. in diameter, densely rusty-tomentulose, the style short. Immature drupe ellipsoid, about 7 mm. long, 4 mm. in diameter.

The Panamanian specimens are sterile, for all practical purposes, and the incomplete floral description is based upon fragmentary collections from South America.

Known as *manwood* and *nispero negro* in Panama. The wood is heavy and extremely durable.

BOCAS DEL TORO: region of Almirante, *Cooper 497*. CANAL ZONE: Gamboa, *Standley 28380*. CHIRIQUÍ: Progreso, *Cooper & Slater 312*.

The cited specimens are, with the exception of some very immature inflorescences, glabrous throughout. In this respect they are unlike their South American counterparts, which are usually rusty-tomentulose throughout.

2. HEISTERIA Jacq.

Heisteria Jacq. Enum. Pl. Carib. 4. 1760.

Rhaptostylum Humb. & Bonpl. Fl. Aequin. 2:139, *t. 125.* 1809.
Hesiodia Vell. Fl. Flum. 4. *t. 140.* 1825, (as *Hesioda*).
Acrolobus Klotzsch, in Verhandl. Akad. Wiss. Berlin 236, *t. 3.* 1856.

Raptostylus Post & O. Kuntze, Lex. Gen. Phaner. 477. 1904.
Phanerocalyx Spencer Le Moore, in Journ. Bot. 59:244. 1921.

Unarmed autotrophic shrubs or trees. Leaves alternate, oval, elliptic or oblanceolate, glabrous, with laticiferous ducts. Inflorescences in compact axillary fascicles, multi-flowered although only 1 or 2 per axil develop into mature fruit. Flowers bisexual, hypogynous, small. Calyx small, generally crateriform, free, 5–6 toothed or lobed, accrescent, becoming coriaceous. Petals 5–6, somewhat connate at the very base, glabrous or puberulent to villous within, valvate in bud. Stamens 10 or 12 in two whorls (in Panamanian species) or 5–6 in one whorl, the anthers globose, dehiscing longitudinally, the filament filiform or liguliform, antipetalous often somewhat shorter than the antisepalous. Ovary superior, conical, 3-merous to the middle, the ovules 3, pendulous, with 2 integuments, the style short to obsolete, the stigma 3-lobed. Fruiting calyx more or less reflexed, often brilliantly colored; drupe globose, oblate spheroid or ellipsoid; embryo embedded in the top of the endosperm, small.

About 65 species, West Africa, Central and South America. Five species are known from Panama.

The genus is generally divided into two sections on the basis of the number of stamens. The five Panamanian species have either 10 or 12 stamens and are therefore placed in section *Euheisteria* Engl. (in Engl. & Prantl Aufl. 2. Nachtr. 19. 1900).

Heisteria is marked by a paucity of flowering specimens which is only partially overcome by a particularly abundant supply of fruiting specimens. Unfortunately, the fruiting structures are rather variable and thus specific delimitation is sometimes obscure.

a. Fruiting calyx much shorter than the drupe; petals puberulent to villous within; filaments puberulent.
- b. Fruiting calyx inconspicuously 5-lobed, about 1 cm. in diameter; drupe oblate spheroid, 7–9 mm. long; fruiting pedicel 13–20 mm. long; petals puberulent within; pistil conical .... 1. H. PATOENSIS
- bb. Fruiting calyx conspicuously 5-lobed, 1.5–2.5 cm. in diameter; drupe broadly ellipsoid, 10–15 mm. long; fruiting pedicel 8–10 mm. long; petals puberulent to villous within; pistil lageniform .... 2. H. CONCINNA

aa. Fruiting calyx as long as or longer than the drupe; petals glabrous within; filaments indefinitely papillate or glabrous.
- c. Leaves linear-lanceolate, 1.5–5.0 cm. broad, gradually tapering to apex, the costa immersed above, emersed below; filaments about 0.25 mm. broad; drupe ovoid, 6–8 mm. long; fruiting pedicel 6–9 mm. long .... 3. H. COSTARICENSIS
- cc. Leaves ovate, elliptic or oblanceolate, 3–8 cm. broad, acute or acuminate at the apex, the costa emersed above and below; filaments about 0.5 mm. broad; drupe ovoid, ellipsoid or obovoid, 5–12 mm. long; fruiting pedicel 8–23 mm. long.
  - d. Leaves oblanceolate to broadly elliptic, 10–27 cm. long, long-acuminate at the apex; anthers 0.5 mm. long and broad; fruiting calyx longer than the drupe, 2–3 cm. in diameter, shallowly 5-lobed; drupe ovoid or ellipsoid; fruiting pedicel 8–12 mm. long. 4. H. MACROPHYLLA
  - dd. Leaves ovate to elliptic or rarely oblanceolate or obovate, 5–15 cm. long, abruptly and briefly acuminate at the apex; anthers about 0.25 mm. long and broad; fruiting calyx about as long as the drupe, 1–2 (–2.5) cm. in diameter, very shallowly 5-lobed or undulate; drupe ellipsoid or obovoid; fruiting pedicel 10–23 mm. long .... 5. H. LONGIPES

1. Heisteria fatoensis Standl. in Field Mus. Nat. Hist. 8:137. 1930.

Shrubs or trees to 3.5 m. tall, the young branches generally angular, sometimes strikingly flexuose, glabrous, brownish-red. Leaves ovate, 5–13 cm. long, 3–6 cm. broad, abruptly and briefly acuminate at the apex, rotund at the base, chartaceous, the costa plane above, emersed below, the primary lateral veins 5–6 pairs; petiole 7–12 mm. long, slightly canaliculate. Calyx crateriform, 5-toothed, glabrous, the teeth 0.5 mm. long and broad; petals 5, deltoid, 1.75–2.0 mm. long, about 1 mm. broad at the base, glabrous without, puberulent within; stamens 10, free, the anthers to 0.25 mm. long and broad, the filaments liguliform, 1.0–1.5 mm. long, about 0.25 mm. broad, puberulent; pistil conical, 0.75–1.0 mm. long, about 0.75 mm. in diameter, glabrous; pedicel 4.5–6.0 mm. long. Fruiting calyx much shorter than the drupe, obscurely lobed, strongly reflexed, about 1 cm. in diameter; drupe oblate spheroid, 7–9 mm. long, 9–11 mm. in diameter, cherry to yellowish-red; pedicel 13–20 mm. long.

Known only from Panama. Flowering and fruiting from July to October.

bocas del toro: Water Valley, *Von Wedel 1401*. colón: Loma de Gloria, near Fató (Nombre de Dios), *Pittier 4244*.

Pittier reports the type collection as being "a woody vine". He may have been mistaken as vines are little known in this genus. In addition, the specimens do not have a vine-like aspect.

2. Heisteria concinna Standl. in Field Mus. Nat. Hist. Bot. 8:137. 1930.

Trees to 9 m. tall, the young branches terete, glabrous, olive-green to brownish-red. Leaves ovate, 6–13 cm. long, 3–6 cm. broad, abruptly and briefly acuminate at the apex, acute to obtuse at the base, coriaceous, the costa plane to immersed above, emersed below, the primary lateral veins generally prominulous; petiole 7–18 mm. long, canaliculate. Calyx crateriform, 5-toothed to the middle, about 1 mm. long, glabrous, the teeth 0.75 mm. long, 0.5 mm. broad; petals 5, elliptic, 2.0–2.5 mm. long, 1.25 mm. broad, glabrous without, the lower half puberulent to villous within; stamens 10, free, the anthers 0.25 mm. long and broad, the filaments filiform, about 1.5 mm. long, puberulent; pistil lageniform, the ovary oblate spheroid, 0.5 mm. long, 0.75 mm. in diameter, the style about 0.75 mm. long; pedicel about 5 mm. long. Fruiting calyx shorter than the drupe, 1.5–2.5 cm. in diameter, reflexed, distinctly 5-lobed, red; drupe broadly ellipsoid, 10–15 mm. long, 8–10 mm. in diameter; pedicel 8–10 mm. long.

Costa Rica and Panama. Flowering and fruiting from December to February at altitudes to 120 meters.

canal zone: Barro Colorado Island, *Woodworth & Vestal 484*. chiriquí: vicinity of San Félix, *Pittier 5197*. veraguas: San Francisco, *Powell s. n.*

3. Heisteria costaricensis Donn. Sm. in Bot. Gaz. 19:254. 1894.

Shrubs to 3 m. tall, the young branches angular, glabrous, olive-green. Leaves linear-lanceolate, 16–25 cm. long, 1.5–5.0 cm. broad, gradually tapering to the apex, acute to obtuse at the base, chartaceous, the costa immersed above, emersed

below, the primary lateral veins numerous; petiole 3–13 mm. long, scarcely canaliculate. Calyx crateriform, deeply 5-toothed, glabrous, the teeth about 0.5 mm. long, 0.5 mm. broad; petals 5, deltoid, about 2 mm. long, 1 mm. broad, glabrous; stamens 10, free, the anthers to 0.5 mm. long and broad, the filaments liguliform, about 1 mm. long, 0.25 mm. broad, glabrous; pistil conical, about 1 mm. long, 1 mm. in diameter; pedicel about 1.5 mm. long. Fruiting calyx longer than the drupe, 1.5–2.5 cm. in diameter, shallowly 5-lobed, somewhat enclosing the drupe or reflexed, red; drupe ovoid, 6–8 mm. long, about 7 mm. in diameter, vertically ribbed, blue; pedicel 6–9 mm. long.

Costa Rica and Panama. In Panama fruiting from October to February.

CANAL ZONE: Quebrada Lopez, *Allen 2128*; along Caño Quebrado, *Pittier 6825*; Barro Colorado Island, *Hunnewell 16422, Standley 40898, 41168.*

4. HEISTERIA MACROPHYLLA Oerst. in Vid. Medd. Kjoebn. 1856:40. 1857.

Heisteria latifolia Standl. in Journ. Wash. Acad. Sci. 17:8. 1927.

Shrubs to 2 m. tall, the young stems terete to somewhat angular, glabrous, olive-green. Leaves elliptic or broadly elliptic to oblanceolate, (5–) 10–37 cm. long, 3–8 cm. broad, acuminate at the apex, acumen to 8 cm. long, cuneate to obtuse at the base, chartaceous to subcoriaceous, the costa emersed above and below, the primary lateral veins numerous, arcuate-ascending; petiole 6–30 mm. long, canaliculate. Calyx crateriform, 5- or 6-toothed, glabrous; petals (4 or) 5, deltoid, about 1.75–2.0 mm. long, 1–2 mm. broad at the base, glabrous; stamens 10, the anthers 0.5 mm. long and broad, the filaments liguliform, 0.75–1.5 mm. long, 0.5 mm. broad, glabrous; pistil conical, 1 mm. long and broad, glabrous; pedicel 1.25–2.0 mm. long. Fruiting calyx as long as or longer than the drupe, 2–3 cm. in diameter, inconspicuously and shallowly 5-lobed, more or less reflexed, red; drupe ovoid or ellipsoid, 8–12 mm. long, 6–9 mm. in diameter, vertically ribbed, black; pedicel 8–12 mm. long.

A common forest species of Central America. Known in Panama as *ajicillo* and fruiting from April to November.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *Von Wedel 1082, 1278*; Fish Creek Mts., *Von Wedel 2269*; Water Valley, *Von Wedel 846, 913, 1538, 1720.* CANAL ZONE: between France Field and Catival, *Standley 30366*; Barro Colorado Island, *Standley 40877.* COLÓN: along Río Culebra, above Santa Isabel, *Pittier 4156.*

Heisteria latifolia was proposed by Standley as a new species primarily on the basis of the very broad leaves with conspicuously elongate petioles. A continuous series between the leaves of *H. macrophylla* and *H. latifolia* can be demonstrated in Panamanian material and therefore it does not seem reasonable to maintain *H. latifolia* as a distinct species.

The flowers appear to be rather variable, even in number of parts. A flower from *Von Wedel 1538* (MO) was found to have 6 calyx lobes, 4 petals and 10 stamens.

Standley reported this species as attaining 10 meters in height (Field Mus. Bot. Ser. 18^{1-2}:409. 1937).

5. HEISTERIA LONGIPES Standl. in Journ. Wash. Acad. Sci. 17:8. 1927.

Shrubs or trees to 20 m. tall, the young branches somewhat angular, glabrous, olive-green. Leaves ovate to elliptic or rarely oblanceolate or obovate, 5–15 cm. long, 3–8 cm. broad, acute to abruptly and briefly acuminate at the apex, acute at the base, chartaceous, the costa emersed above and below, the primary lateral veins numerous; petiole 5–15 mm. long, deeply canaliculate. Calyx crateriform, 5-lobed to one-third from the base, glabrous; petals 5, deltoid, 2.25–2.75 mm. long, 1.25–1.5 mm. broad, glabrous; stamens 10, free, the anthers about 0.25 mm. long and broad, the filaments liguliform, about 1.5 mm. long, 0.5 mm. broad, glabrous or indefinitely papillate; pistil conical, 1 mm. tall, 1.25 mm. in diameter; pedicel 3.5–4.0 mm. long. Fruiting calyx about as long as the drupe, 1.0–2.0 (–2.5) cm. in diameter, shallowly 5-lobed or undulate, generally somewhat reflexed, red; drupe ellipsoid or obovoid, 5–10 (–12) mm. long, 5–7 mm. in diameter; pedicel 10–23 mm. long.

Fruiting from January to September to 2000 meters. Known as *naranjillo colorado* in Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 444, 567, Cooper & Slater 127*; region of Almirante, *Cooper 569*; Old Bank Island, *Von Wedel 2123*; Isla de Colón, *Woodson, Allen & Seibert 1945*. CANAL ZONE: along the Trinidad River, *Pittier 4006*; Tortuguilla cove (area west of Limón Bay, Gatún Locks and Gatún Lake), *Johnston 1523*; Barro Colorado

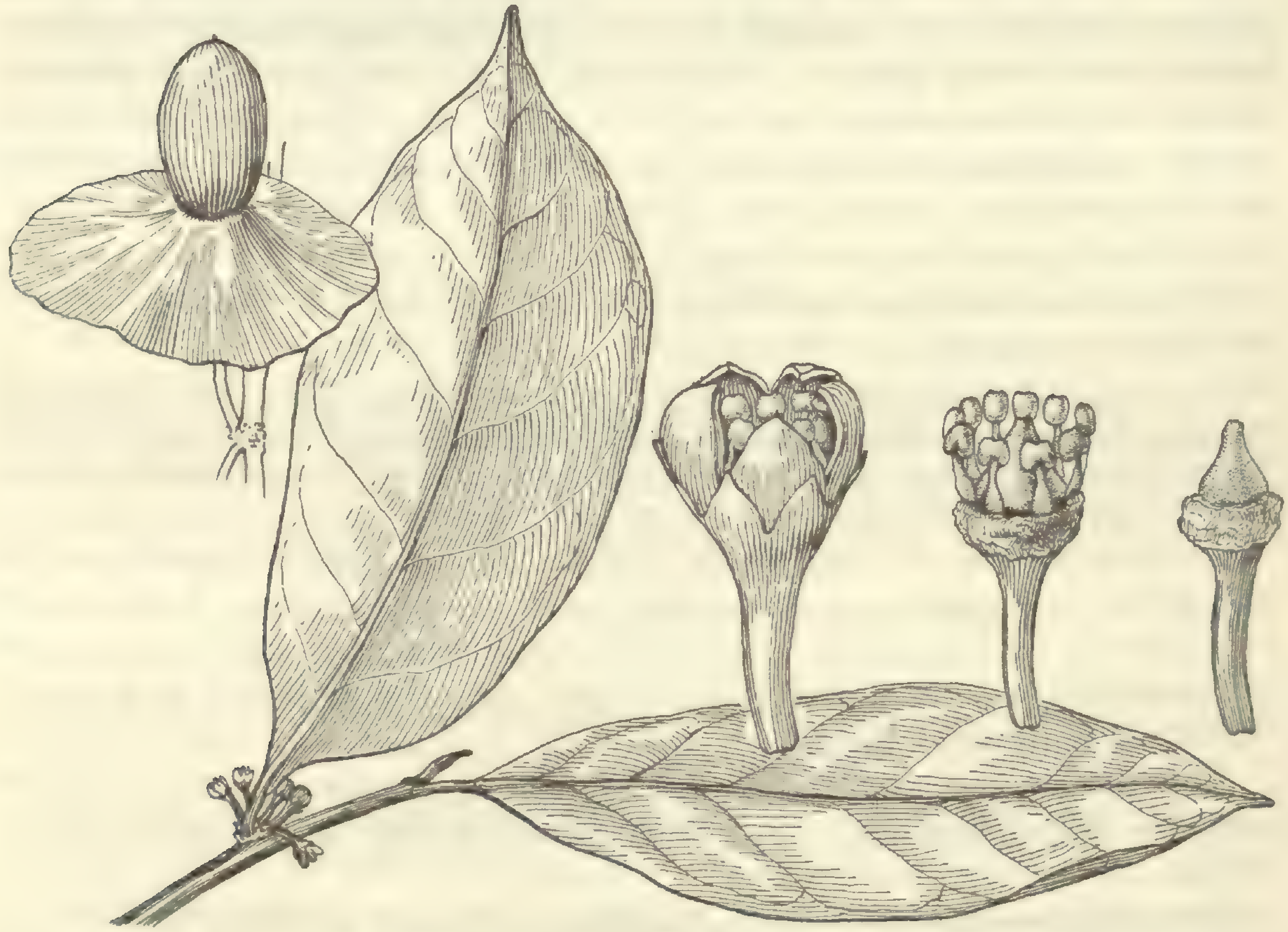

Fig. 84. *Heisteria longipes*

Island, *Bailey & Bailey 81*, *Bangham 534*, *Kenoyer 341*, *Salvoza 923*, *958*, *Wetmore & Abbe 20*, *99*, *Wilson 153*, *Woodworth & Vestal 436*. CHIRIQUÍ: vicinity of Puerto Armuelles, *Woodson & Schery 856*, *Stern & Chambers 126*; trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, *Allen 1589*; Progreso, *Cooper & Slater 166*. COCLÉ: El Valle de Antón, along Río Indio trail, *Hunter & Allen 328*. DARIÉN: near the mouth of Río Yapé, *Allen 339*. PANAMÁ: Cerro Campana, trail from Campana to Chica, *Allen 2657*. SAN BLAS: high hills back of Puerto Obaldía, *Pittier 4289*.

The type specimen, *Pittier 4006* (US), is an unusual specimen for two reasons: the petals and stamens which are ordinarily caducous have persisted into young fruit formation; secondly, Standley reported 6 petals and 12 stamens for it. Examination of the immature fruit of this specimen revealed only 5 petals and 10 stamens although there appeared to be some peculiarities in the androecial whorl, namely, basal cohesion between some of the filaments. Such floral variability upon a single specimen is entirely possible and has been demonstrated in at least one other species from Panama, *H. macrophylla* Oerst.

3. XIMENIA L.

XIMENIA L. Sp. Pl. 1193. 1753.

Heymassoli Aubl. Hist. Pl. Guyan. Franç. 1:324, *t. 125*. 1775.
Rottboelia Scop. Introd. 233, n. 1060. 1777.
Pimecaria Raf. Alsog. Am. 64. 1838.

Armed root parasitic shrubs or trees, the spines axillary, the young branches glabrous. Leaves alternate, ovate or elliptic, mucronate or acuminate at the apex, obtuse to cuneate at the base. Inflorescence umbellate, simple or compound, sometimes fasciculate, bracteate. Flowers bisexual, hypogynous, medium-sized. Calyx small, 3- to 5-toothed, not accrescent. Petals 4 or 5, free, thickly covered with red-brown barbed hairs within, valvate in bud. Stamens 8–10, in two whorls, the anthers oblong or linear, dehiscing longitudinally, the filaments filiform. Ovary long-conical, 4-loculate above the middle, the ovules pendulous, with 1 integument, the style filiform, about as long as the ovary, the stigma minutely capitate. Drupe ovoid to ellipsoid, from yellow to purple; seed with a small embryo at the apex of the fleshy endosperm.

Approximately 15 species, circumtropical; Florida, Central and South America, Antilles, Africa, East Indies, Asia, and Australia. Only one species known from Panama.

1. XIMENIA AMERICANA L. Sp. Pl. 1193. 1753.

Ximenia multiflora Jacq. Enum. Pl. Carib. 19. 1762.
Ximenia inermis L. Sp. Pl. ed. 2. 497. 1762.
Ximenia aculeata Crantz, Inst. 2:381. 1766.
Heymassoli spinosa Aubl. Pl. Guayan. Franç. 1:324, *t. 125*. 1775.
Ximenia elliptica Forst. f. Prod. 27. 1786.
Ximenia spinosa Salisb. Prod. 276. 1796.
Ximenia montana Macfad. Fl. Jamaica 1:121. 1837.

Ximenia loranthifolia Span. in Linnaea 15:177. 1841.
Ximenia arborescens Tussac, ex Walp. Rep. 1:377. 1842.
Ximenia laurina Delile, in Ann. Sci. Nat. ser. 2. 20:89. 1843.
Ximenia fluminensis M. Roem. Syn. Hesper. 22. 1846.
Ximenia oblonga Lam. ex Hemsl. in Biol. Centr. Am. Bot. 1:185. 1879.

Trees to 7 m. tall, the spines axillary branches, often leafy, usually stout. Leaves ovate, 3–11 cm. long, 2.0–4.5 cm. broad, retuse and mucronulate at the apex, obtuse to cuneate at the base, subcoriaceous, glabrous or bullate, the costa immersed above, emersed below, the primary lateral veins 3–6 pairs, most conspicuous towards the base of the lamina; petiole 5–7 mm. long, canaliculate. Inflorescence umbellate, simple or compound, often fasciculate, multi-flowered, the bracts small, ciliate, caducous. Calyx crateriform, to 0.75 mm. long, about 1.5 mm. in diameter, 3- or 4-toothed, ciliate; petals 4, liguliform, 7–11 mm. long, 1.5–2.0 mm. broad, greatly reflexed, coriaceous, glabrous without, densely covered with red-brown barbed hairs within, white and often purple tipped; stamens 8, subexserted, the anthers linear, 3.0–4.5 mm. long, 0.5–0.75 mm. broad, the filaments 3.0–4.5 mm. long, glabrous; ovary long-conical, 3–4 mm. long, 1.0–1.5 mm. in diameter, glabrous, the style 3.0–4.5 mm. long; pedicel 5–6 mm. long. Drupe ellipsoid, 2–3 cm. long, 1.5–2.5 cm. in diameter, pale yellow.

A circumtropical species.

Fig. 85. *Ximenia americana*

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *Von Wedel 1402*; Water Valley, *Von Wedel 1620*. CANAL ZONE: vicinity of Fort Sherman, *Standley 31145*; Victoria Fill, *Allen 1750*. CHIRIQUÍ: Isla Parida, *Pittier 2819*. DARIÉN: Patiño, on cliffs along beach, *Pittier 5703*; vicinity of La Palma, *Pittier 5498*. PANAMÁ: San Jose Island, *Erlanson 149, Johnston 719, 774*; Bella Vista, *Killip 39943*; Nuevo San Francisco, *Standley 30780*. PROVINCE UNKNOWN: Bahia Honda, *Elmore H39*; La Venta, *Hunnewell 16417*.

4. SCHOEPFIA Schreb.

SCHOEPFIA Schreb. Gen. 129. 1789.

Codonium Rohr, ex Vahl, in Skrivt. Natur. Selsk. Kjoeb. 2:206, *t. 6.* 1792.
Haenkea Ruiz & Pavon, Fl. Per. 3:8, *t. 231.* 1802.
Diplocalyx A. Rich. in Sagra, Hist. Cuba 11:81. 1850.
Ribeirea F. Allemão, Trab. Comm. Sc. Expl. Bot. Rio de Janeiro 29, 38. 1864.
Schoepfiopsis Miers, in Journ. Linn. Soc. 17:75. 1878.

Unarmed glabrous shrubs or trees, reportedly root parasites. Leaves alternate, entire, coriaceous. Inflorescences few-flowered racemes generally fasciculate in the leaf axils, with or without basal perular bracts and the flowers subtended by a cupule composed of 2 bracteoles and 1 bract or subtended by a single bract.

Fig. 86. *Schoepfia schreberi*

Flowers bisexual, small. Calyx extremely small, cyathiform or crateriform, margin subentire. Petals 3–6, united into a tubular-campanulate corolla, often pubescent within, the lobes valvate, reflexed, white, yellow or red. Stamens 3–6, in one whorl, as many as the petals, antipetalous, adnate to the corolla, the anthers oval, dehiscing longitudinally, sessile or short-filamented. Ovary half-immersed, the ovules pendulous, lacking integument, the style thin, the stigma 2- or 3-lobed. Spurious fruit with the drupe enclosed in the adnate, accrescent calyx, eccentrically annulate at the apex; seed with the small embryo at the tip of the endosperm.

About 38 species of the Old and New World. Only one species is definitely known from Panama. A second species, S. *vacciniiflora*, has been reported by Standley (in Field Mus. Nat. Hist. Bot. 18^2:409. 1937 and in Fieldiana Bot. 24^4:90. 1946) in Panama. The S. *vacciniiflora* name is in itself a confusing matter. *Schoepfia vacciniiflora* Planch. ex Hemsl. (Diag. Pl. Mex. 5. 1878) is reported from Guatemala whereas S. *vacciniiflora* Planch. ex Planch. & Triana (Ann. Sci. Nat. ser. 5. 15:382. 1872) is reported from Colombia. Whether or not these epithets are based upon a common species is difficult to determine.

1. Schoepfia schreberi J. F. Gmel. Syst. Veg. 2:376. 1791.

Schoepfia americana Willd. Sp. Pl. 1:996. 1798.
Schoepfia arborescens Roem. & Schult. Syst. 5:160. 1819.

Shrubs or trees to 8 m. tall, the young branches slender, angular, olive-green to white. Leaves ovate to lanceolate, 4–8 cm. long, 1.5–3.5 cm. broad, acute-acuminate to acuminate at the apex, cuneate-attenuate or obtuse at the base, the costa emersed above and below, the primary lateral veins 5–6 pairs, rather conspicuous; petiole to 5 mm. long. Inflorescences 1- to few-flowered, fasciculate, the peduncle to 5 mm. long, the flowers subtended by a cupule composed of 2 bracteoles and 1 bract, the cupule 1–3 mm. in diameter, 3-toothed, ciliate. Calyx cyathiform, about 1 mm. long, subentire, glabrous; corolla tube 2.0–2.5 mm. long, 1.5–2.5 mm. broad at the orifice, glabrous, red, the lobes 4 or 5, deltoid, 1.0–1.5 mm. long and broad, glabrous without and minutely puberulent within except for a cluster of villous hairs at the point of staminal insertion; stamens 4 or 5, inserted at the orifice of the corolla tube, the anthers 0.5–0.75 mm. long and broad, exserted, subsessile; ovary half-inferior, globose, densely papillate, the style 0.5 mm. long, the stigma bifid, included. Spurious fruit ellipsoid, 10–13 mm. long, 7–8 mm. in diameter, glabrous.

Florida, Central America, Antilles and South America.

CHIRIQUÍ: vicinity of El Boquete, *Maxon 5040*. COCLÉ: Penonomé and vicinity, *Williams 333*. PANAMÁ: Bejuco, *Allen 978*.

BALANOPHORACEAE

By LORIN I. NEVLING, Jr.

Fleshy root parasites, rhizomatous, lacking chlorophyll, the rhizome tuberous, digitiform, cylindrical or filiform, sometimes branched, naked or sometimes with scale-leaves, yellow to dark red in color. Inflorescence monoecious or dioecious, highly modified, of endogenous origin, above ground at anthesis, more or less erect, sessile or pedunculate (in our species), the peduncle terete, with or without an encircling, often basal sheath, scaly or naked above the sheath, the head with or without protective peltate scales, sometimes with paraphysoid trichomes or reduced pistillate flowers surrounding or subtending the flowers. Flowers unisexual, monochlamydeous, small. Perianth absent or more often present, of 2–4 (–8) tepals, free or connate into a tube of varying size and shape, in pistillate flowers sometimes reduced to an epigynous collar or absent. Stamens generally as many as perianth segments and opposite them, the filaments free or connate into a staminal column of varying length, sometimes very short, the anthers free or connate into a syandrium, introrse or extrorse; absent in pistillate flowers. Pistil composed of 1, 2 (or 3) carpels, the ovules usually 1 per carpel, lacking integument, often fused to the wall of the ovary, the styles 1 or 2, terminal, the stigma usually simple, rarely sessile; in staminate flowers absent or reduced to a pistillode. Fruit nut-like or drupaceous, the endocarp usually hard; seed sometimes fused to the wall of the fruit, the embryo apical in the fleshy oil-rich endosperm, with or without suspensor.

Approximately 18 genera, pantropic but primarily distributed in the Southern Hemisphere. Three genera are represented in Panama.

a. Inflorescence monoecious or rarely dioecious, the peduncle with or without an encircling sheath, otherwise naked, the head when immature covered with deciduous, 6-sided, peltate scales, the staminate and pistillate flowers surrounded by claviform, paraphysoid trichomes; staminate flowers with the perianth segments connate at least in the lower half, the anthers completely connate, a small pistillode sometimes present; pistillate flowers with the pistil 2-carpellate, the styles 2, spreading; fruit ovoid, ellipsoid or obovoid, compressed.

b. Staminate flowers with perianth of 3 (–6) tepals, connate in the lower half into a tube, the lobes becoming widely reflexed, the filaments adnate to the perianth below, free or connate below into a staminal column, usually free above, the anthers each with two posterior pollen sacs and one anterior pollen sac.................................. 1. Helosis

bb. Staminate flowers with the perianth segments completely connate, the margin crenate, the filaments free from the perianth, completely connate, the anthers each with 2 large lateral pollen sacs.................. 2. Corynaea

aa. Inflorescence dioecious or rarely monoecious, the peduncle with an encircling basal sheath, scaly, the head when immature covered by the imbricate peduncle scales, the staminate flowers subtended by reduced pistillate flowers, the pistillate flowers agglutinate into a dense mat, ebracteate; staminate flowers with the perianth segments free, the anthers connate below, free above, pistillode absent; pistillate flowers with the pistil 1-carpellate, the style 1, erect; fruit ellipsoid, never compressed.. 3. Langsdorffia

1. HELOSIS Rich.

Helosis Rich. in Mém. Mus. Par. 8:416, *t. 20*. 1822, nom conserv.

Caldasia Mutis, ex Caldas, in Seeman. Nuev. Gran. 2:26. 1810, nom. rejic.
Latraeophila Leandr. Sacram. ex St. Hil. in Ann. Sci. Nat. ser. 2. 7:32. 1837.
Lathraeophila Hook. f. in Trans. Linn. Soc. 22:55. 1856.

Rhizome filiform to digitiform, often intertwined, rich in starch, yellowish to brownish. Inflorescence monoecious, claviform, the peduncle thick, generally encircled at the base or at the middle with a glabrous, toothed to lobed, oblique sheath (rarely absent), the head globose, ovoid or ellipsoid, when immature covered with 6-sided, peltate, umbonate scales beneath which occurs a dense mat of paraphysoid trichomes and young developing flowers, the scales spirally arranged, deciduous, about the axis of each scale are oriented two whorls containing many pistillate flowers surrounded by a single whorl of 6 flowers which are situated at the angles of the covering scale and are either rudimentary or functionally staminate. Perianth in the staminate flowers composed of 3 (or 6) tepals connate in the lower half into a tube, the lobes becoming widely reflexed; in the pistillate flowers reduced to a low bilabiate epigynous collar or, according to some authors, absent. Stamens as many as the perianth lobes and opposite them, exserted, the filaments adnate to the perianth tube below, free or connate into a staminal column, generally free above, the anthers united into a synandrium, each with two posterior and a single anterior pollen sac, introrse; absent in the pistillate flowers. Pistil 2-carpellate, the ovary compressed, the ovules 2, fused to the ovary wall, generally only one maturing, the styles 2, filiform, spreading, deciduous, the stigmas globose or capitate; pistillode sometimes present in the staminate flowers, often very reduced. Fruit nut-like, compressed, with crusty epicarp and hard endocarp.

Howard (in Rhodora 61:79–81. 1959) reports that in alcohol-preserved specimens of *Helosis* from the West Indies the filaments are free throughout their length whereas in herbarium specimens the filaments appear to be tightly adherent. In contrast, in herbarium specimens from Central America the filaments appear to be adnate at least at the base; this same basal adnation also is found in alcohol-preserved specimens.

Three species from the Antilles and tropical America. A single species from Panama.

1. Helosis mexicana Liebm. in Forh. Vidensk. Skand. Nat. 4:181. 1844.

Helosis aquatica Mutis, ex Hook f. in Trans. Linn. Soc. 22:59. 1856.
Caldasia mexicana (Liebm.) O. Kuntze, Rev. Gen. 2:590. 1891.

Rhizome and inflorescence more or less ferrugineous on drying. Inflorescence with the peduncle 8–16 cm. long, with or without an encircling sheath, the head ovoid or more often ellipsoid, 3–5 cm. long, 1.5–3.0 cm. in diameter, the scales about 3 mm. in diameter, stalk about 2 mm. long, the paraphysoid trichomes claviform, 1.0–2.5 mm. long. Staminate flowers: perianth tube tubular, 2–3 mm. long, glabrous, the lobes 3, ovate, 1–3 mm. long, 0.75–1.0 mm. broad; filaments connate, free at the apex at maturity, 0.25–0.75 mm. long, the synandrium 0.5–1.0 mm.

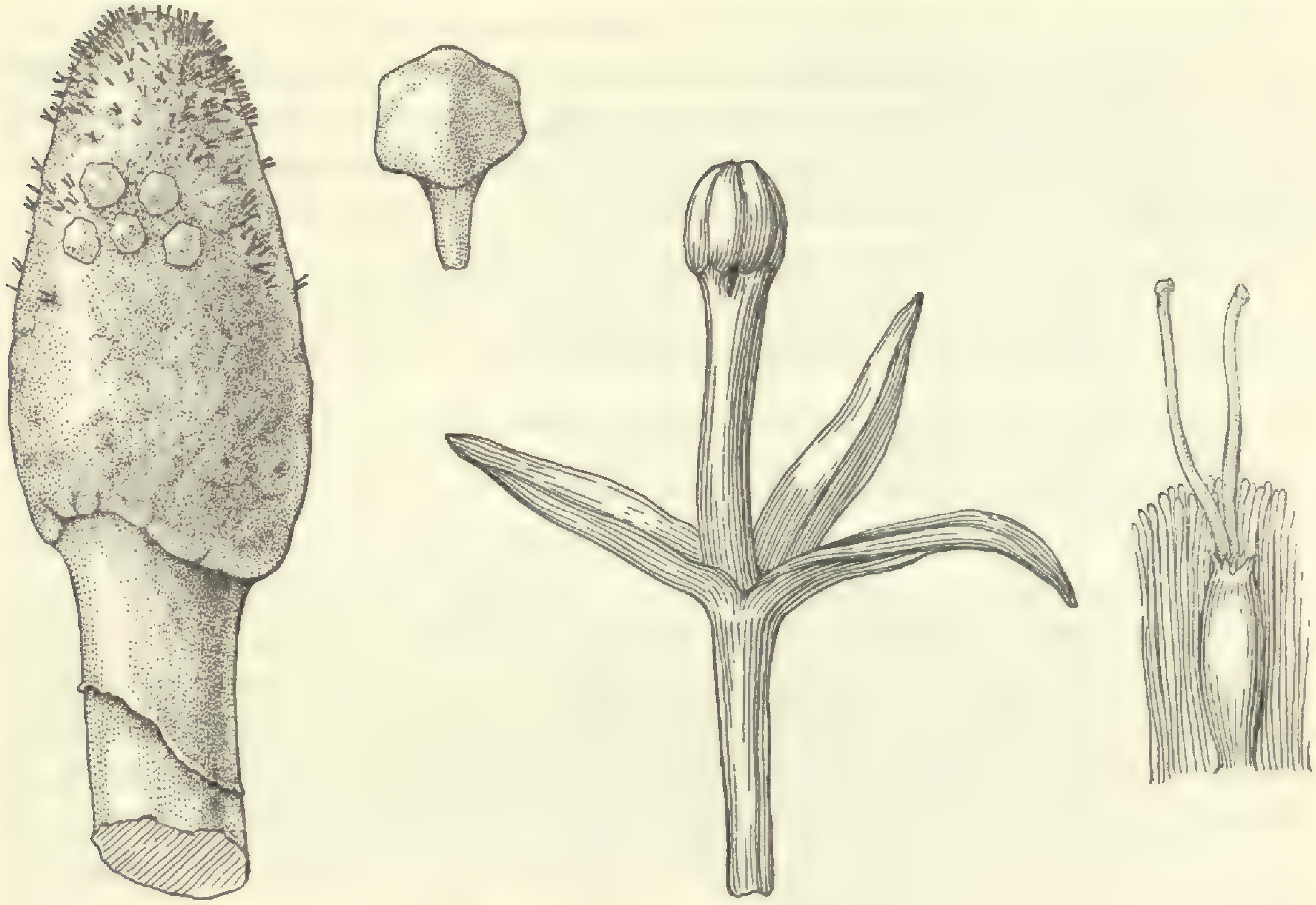

Fig. 87. *Helosis mexicana*

long, 0.5–0.75 mm. in diameter. Pistillate flowers based on Mexican specimens: perianth obscurely bilabiate and becoming fimbriate, minute; ovary tubular to somewhat ellipsoid, 1.0–1.25 mm. long, glabrous, the styles 1.25–1.75 mm. long, deciduous, the stigmas minutely capitate. Fruit 1.25–2.25 mm. long, about 0.5 mm. broad.

CANAL ZONE: Matachín, *Kuntze 74*. COCLÉ: El Valle de Antón, *Seibert 469*.

2. CORYNAEA Hook. f.

CORYNAEA Hook. f. in Trans. Linn. Soc. 22:31, *t. 13, 14*. 1856.

Itoasia O. Kuntze, Rev. Gen. 2:590. 1891.

Rhizomes nodular or rarely elongate, often lobed, lacking scales, sometimes with root-like processes. Inflorescence mostly monoecious and proterogynous or rarely dioecious, claviform, the peduncle encircled at the base with a glabrous annular to cupuliform sheath which is sometimes very obscure, naked above the sheath, the head globose or ellipsoid, when immature covered with 6-sided, peltate, umbonate scales underneath which occurs a dense mat of paraphysoid trichomes and young developing flowers, the scales deciduous prior to anthesis. Perianth of the staminate flowers tubular, conical or subcampanulate, completely connate, crenate; in the pistillate flowers reduced to a low epigynous collar or, according to some authors, absent. Stamens 3, exserted, the filaments completely fused into a

staminal column free from the perianth tube, the anthers united into a synandrium, each with two large lateral pollen sacs, introrse; absent in the pistillate flowers. Pistil 2-carpellate, the ovary compressed, the ovules 2, fused to the ovary wall, generally only one maturing, the styles 2, filiform, spreading, deciduous, the stigmas globose or capitate; pistillode present in the staminate flowers. Fruit nutlike, compressed, with crusty epicarp and hard endocarp.

A poorly known genus consisting of perhaps 4 species of Central and South America. Only 1 species is represented in Panama.

1. Corynaea crassa Hook. f. in Trans. Linn. Soc. 22:31, *t. 13, 14.* 1856.

Itoasia crassa (Hook. f.) O. Kuntze, Rev. Gen. 2:590. 1891.

Rhizome an irregularly multi-lobed mass, becoming ferrugineous upon drying. Inflorescence pink, the peduncle with an irregularly short-lobed, basal sheath, 1.5–2.5 cm. long, vertically ribbed, glabrous, the head globose and becoming fusiform, 2–4 cm. long, 1.5–2.0 cm. in diameter, the scales 3–4 mm. in diameter, stalk 2–3 mm. long, the paraphysoid trichomes claviform, 1.5–2.0 mm. long. Staminate flowers not seen. Pistillate flowers: perianth a low epigynous collar or absent (?); ovary obovoid, 1 mm. long, 0.5–0.75 mm. broad, the styles 1.0–1.5 mm. long, the stigmas minutely capitate; pedicel to 0.5 mm. long. Fruit obovoid, about 1.5 mm. long, 1 mm. broad.

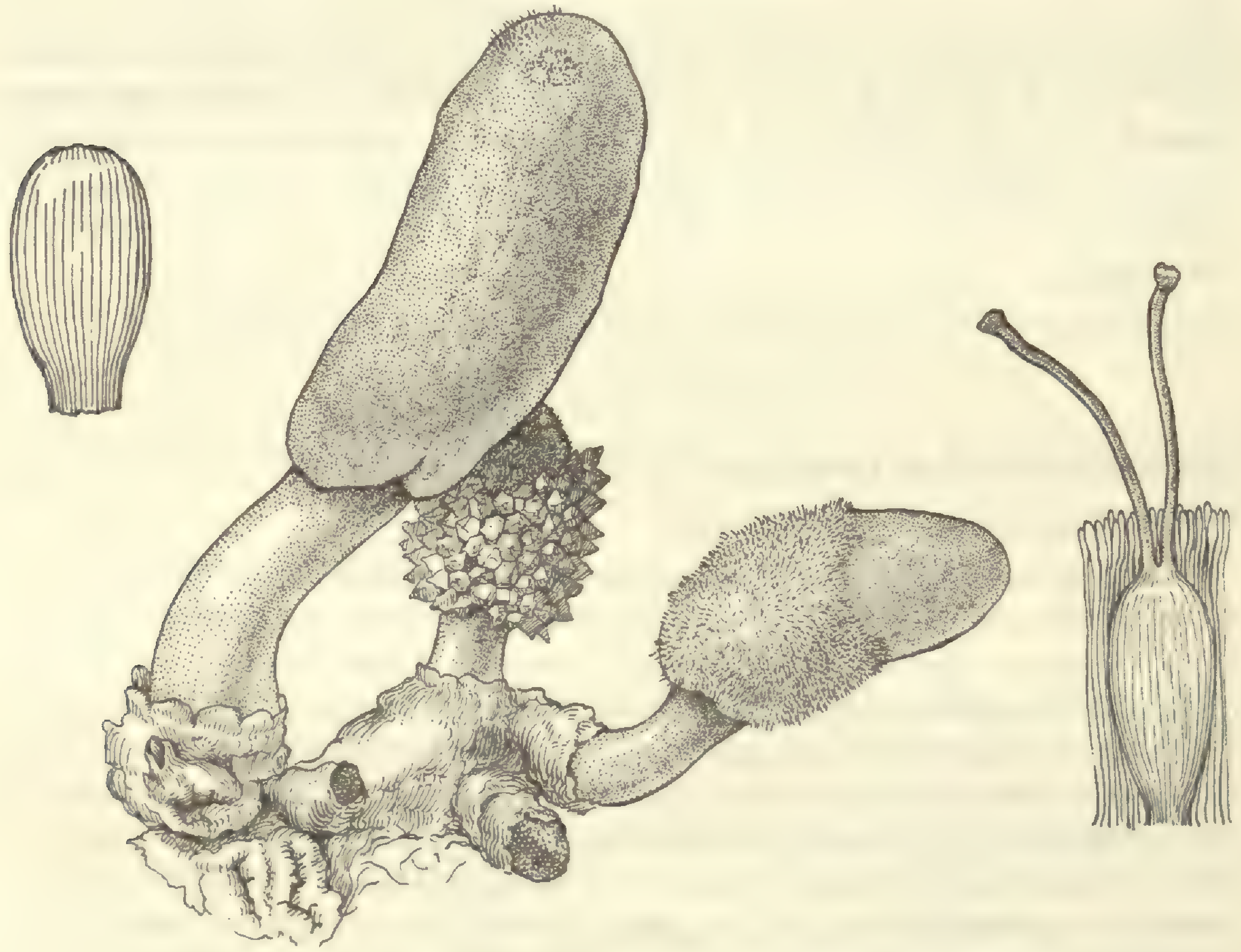

Fig. 88. *Corynaea crassa*

Collected flowering in July between 3500 and 4000 meters. According to Woodson and Schery these plants are parasitic on bamboo roots.

CHIRIQUÍ: Potrero Muleto to summit, Volcán de Chiriquí, *Woodson & Schery 470.*

3. LANGSDORFFIA Mart.

LANGSDORFFIA Mart. in Eschweg. Journ. Bras. 2:178. 1818.

Langsdorfia C. A. Agardh, Aphor. 203. 1825.
Senftenbergia Klotzsch & Karst. ex Klotzsch, in Linnaea 20:460. 1847, nom. nud. in synon.

Rhizome lobed, creeping or upright, often dichotomously branched, tomentose and sometimes glabrescent. Inflorescence dioecious or rarely monoecious, capitate to clavate, the peduncle terete, thick, enclosed at the base by a short, lobed or toothed sheath, above the sheath vested with many imbricate scales, the scales in the basal portion ovate to oval-lanceolate, gradually becoming progressively lanceolate towards the flower-head, the head globose, ovoid or ellipsoid, staminate generally larger than the pistillate, yellow, yellowish-red or red, the staminate flowers subtended by reduced pistillate flowers, the pistillate flowers agglutinate into a dense mat, ebracteate. Perianth in the staminate flowers composed of 3 or rarely 2 concave tepals, valvate; in the pistillate flowers reduced to an epigynous collar, obscurely 2- or 4-lobed. Stamens as many as the tepals and opposite them, exserted, the filaments short, connate into a staminal column, the anthers connate below and free above, each with 4 pollen sacs at the base and 2 at the apex, extrorse; absent in the pistillate flowers. Pistil 1, the ovules 1, fused to the ovary wall, the style 1, erect, filiform, deciduous, the stigma minutely papillate; pistillode absent in the staminate flowers. Fruit drupaceous, with fleshy epicarp and hard endocarp.

Apparently only a single species from Mexico to southern Brazil.

1. LANGSDORFFIA HYPOGAEA Mart. in Eschweg. Journ. Bras. 2:178, *t. 5.* 1818.

Langsdorffia janeirensis Rich. in Mém. Mus. Par. 8:412, *t. 19.* 1822.
Langsdorffia moritziana Klotzsch & Karst. in Linnaea 20:461. 1847.
Thonningia janeirensis (Rich.) Liebm. in Forh. Skand. Naturf. Christ. 180. 1847.
Thonningia mexicana Liebm. loc. cit. 1847.
Langsdorffia rubiginosa Wedd. in Ann. Sci. Nat. ser. 3. 14:187. 1850.
Senftenbergia moritziana (Klotsch & Karst.) Eichl. in Mart. Fl. Bras. 4^2:10. 1869, nom. nud. in synon.

Rhizome digitiform, canescent-tomentose. Staminate inflorescence clavate, the peduncle 2–5 cm. long, scaly, surrounded at the base by a lobed sheath, the lobes deltoid, 0.5–1.0 cm. long and broad, canescent-tomentose, the scales stiff, ciliate, enclosing the head when immature, lower scales ovate, about 1 cm. long, 5–7 mm. broad, upper scales lanceolate, to 3.5 cm. long, 1 cm. broad, the head ellipsoid, 5–7 cm. long, about 3 cm. in diameter. Staminate flowers based on Brazilian specimens: pedicel 6–10 mm. long; tepals 3 (or 2), free, ovoid, about 3 mm. long, 1.5–2.0 mm. broad, becoming widely reflexed, glabrous; stamens 3, the filaments about 0.5 mm. long, completely connate, the anthers connate below, free above. Pistillate inflorescence generally capitate to clavate, the peduncle and vesture as in the staminate inflorescence, the head subglobose, 2–4 cm. long, 4.5 cm. in diameter. Pistillate flowers: free but tightly agglutinated with one another above due to a

waxy secretion; perianth epigynous, connate into a curious tubular or obovoid structure, 1.5–2.5 mm. long, 0.5–0.75 mm. in diameter, surrounding the style and in intimate contact with it, the perianth lobes 2, short; ovary ellipsoid, about 1 mm. long, 0.5 mm. in diameter, the style 1, 0.5–1.5 mm. long, slender, spirally twisted, the stigma minutely capitate. Fruit ellipsoid, about 1 mm. long, 0.5 mm. in diameter.

The only specimen examined was collected flowering and fruiting in July at an altitude of 2000–2500 meters.

CHIRIQUÍ: forested ridges south of Finca Lérida, *Allen 4773*.

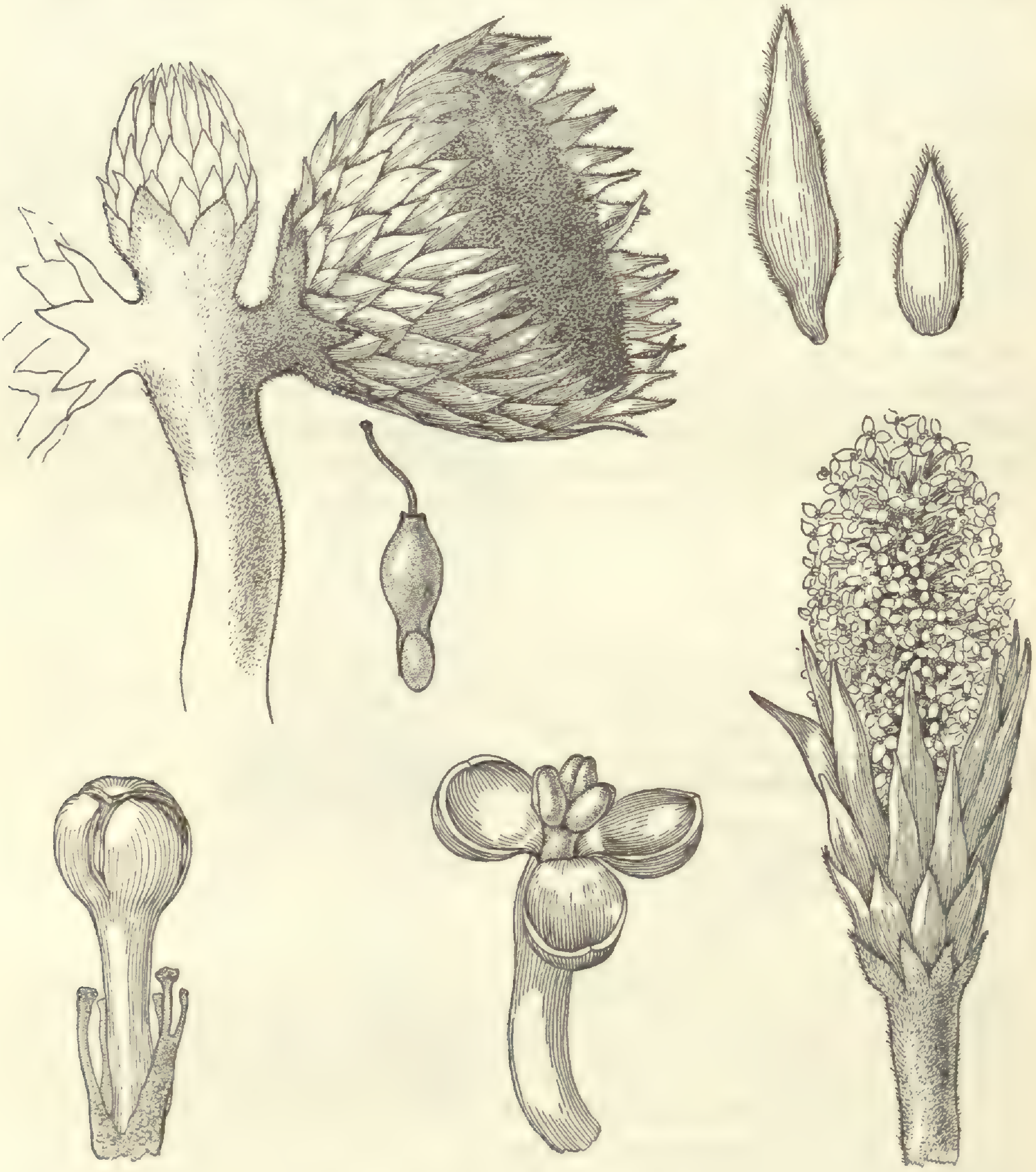

Fig. 89. *Langsdorffia hypogaea*

ARISTOLOCHIACEAE

BY HOWARD WM. PFEIFFER

Scandent lianas, herbs, or rarely trees, the wood often having broad interfascicular rays. Leaves alternate, spiral, estipulate, simple, palmately veined, usually entire. Flowers mostly axillary, perfect, actinomorphic or zygomorphic, hypogynous to epigynous, in racemes, cymes, solitary or in clusters and cauliflorous, rarely terminal, large and showy or small, often with fetid or resinous odor. Calyx gamosepalous, often petaloid and elaborately contorted and lobed. Corolla of 3 reniform petals in *Saruma*, rudimentary in some species of *Asarum*, absent in all other members of the family. Stamens 6 to 12 or occasionally many, in one or two whorls, free, connate or adnate to the short, fleshy, united styles. Ovary apocarpous to syncarpous, 6- to 4-carpellate and -loculate, with marginal to axile placentation; ovules many to few, anatropous. Pollen monosulcate to nonaperturate, spherical. Fruit follicular or capsular with septicidal, rarely septifragal or irregular dehiscence, often dehiscing acropetally; seeds numerous to few, with a small basal embryo in abundant endosperm.

The Aristolochiaceae, or Birthworts, are distributed throughout the tropic and temperate regions of the world. The genera are poorly defined and are in need of competent revision. The largest genus, *Aristolochia*, is the sole representative of the family in Panama. It is a large genus with about 300 species in tropic and temperate areas throughout the world. Eleven species are reported from Panama, but further collections will probably double this number.

The leaves of *Aristolochia* are remarkably variable. For example, on a single shoot about 2 dm. long of *Aristolochia panamensis* leaves may be seen which are narrowly linear-lanceolate, broadly ovate, and broadly obtriangulate with a deeply emarginate apex. As a consequence, leaf characteristics have been used as infrequently as possible in the keys. An exception to this general rule may be noted in that group which bears pseudostipules. The Aristolochiaceae, it will be recalled, are estipulate; however, in these species, an axillary bud produces a single, small leaf which is amplexicaul and nearly sessile. It frequently is ruffled, not having the shape of the ordinary leaves on the shoot, and looks strikingly like a pair of connate, auriculate stipules.

The description of a flower as complex as that of *Aristolochia* is always a problem. The species differences of greatest importance lie in the elaborate inflations and expansions of the calyx tube. In an attempt to standardize the descriptions, therefore, it has seemed convenient to subdivide the calyx tube into several morphological portions and to treat each of these separately. It should be emphasized here that not necessarily all of these subdivisions are present in any given species.

An explanation of these arbitrary designations follows. As the calyx arises from the apex of the ovary, it expands into a large, inflated, usually gibbous portion called the *utricle*. The utricle narrows into the cylindrical portion known as the *tube*. This expands and usually imperceptibly merges with the expanded *limb*. In

the larger flowers the tube has a peculiar venation at its distal end which subdivides the tube into two portions, conveniently described as the *tube proper,* and the *throat.* The throat is usually funnelform and as a result tends to lend greater width and expansion to the limb.

One constantly finds reference in the literature to the fetid odor of *Aristolochia* flowers. While many of them are truly fetid and evil smelling, many are odorless and a few have been described as having either a sweet or a resinous odor. The flowers ostensibly are pollinated by various species of Diptera. In herbarium specimens, dissection of the utricle often reveals insects which have burrowed or forced their way between the lobes of the styles. The flowers are equipped with rigid, inward-pointing hairs throughout the length of the tube. The Diptera, doubtless attracted by the color and odor of the blooms, are trapped within the utricle since they are able to pass only inward over the hairs. The flowers are protogynous. With pollination, the anthers dehisce and the rigid hairs in the tube wilt, allowing the flies to escape and carry pollen to another bloom.

Several species of *Aristolochia* furnish the serpentaria of medicine which is used as a tonic and as a febrifuge. Many of the plants are utilized as a native remedy for snakebite and bear the common name Snakeroot.

The remarkable shapes of the calyx tubes lead to various names such as Dutchman's Pipe, Pelican Flower and Goose Flower. The name *Aristolochia,* which is derived from the Greek *aristos,* best, and *lochia,* delivery, refers to its supposed medicinal properties in connection with the alleviation of the pains of childbirth; the curved flower, with summit and base together suggesting, by the doctrine of signatures, the human fetus in the womb.

Standley, writing about the aristolochias of El Salvador, reports that the roots of *guaco* or *A. anguicida* are used by the natives to wash clothes, to scour out dirt, and also as a remedy for stomach ache. He further states that infusions of *A. arborescens* are used as a remedy for venereal diseases in the female and for dysentery in children.

1. ARISTOLOCHIA L.

Aristolochia L. Sp. Pl. ed. 1. 960. 1753.

Isotrema Raf. in Amer. Monthly Mag. & Crit. Rev. 4:195. 1819.
Hocquartia Dum. Comm. Bot. 30. 1822.
Dasyphonion Raf. First Cat. Bot. Gard. Transylv. Univ. 13. 1824.
Cardiolochia Raf. ex Rchb. Consp. 85. 1828.
Einomeia Raf. Medic. Fl. 1:62. 1828.
Endodeca Raf. loc. cit. 62. 1828, sphalm.
Pistolochia Raf. loc. cit. 62. 1828.
Siphisia Raf. loc cit. 62. 1828.
Isiphia Raf. Medic. Fl. 2:232. 1830.
Dictyanthes Raf. in Loudon, Gard. Mag. 8:247. 1832.
Niphus Raf. loc. cit. 247. 1832.
Siphidia Raf. loc. cit. 247. 1832.
Ambuya Raf. Fl. Tellur. 4:98. 1836.
Diglosselis Raf. loc. cit. 98. 1836.
Endotheca Raf. loc. cit. 98. 1836, corr. *Endodeca* (1828).

Hexaplectris Raf. loc. cit. 97. 1836.
Plagistra Raf. loc. cit. 98. 1836.
Psophiza Raf. loc. cit. 99. 1836.
Pteriphis Raf. loc. cit. 99. 1836.
Tropexa Raf. loc. cit. 98. 1836.
Guaco Liebm. in Forhandl. Skandin. Naturf. 1844:203. 1847.
Howardia Klotzsch, in Monatsb. Acad. Berl. 1859:607. 1859.

Lianas, rarely upright perennial herbs, shrubs or trees. Leaves alternate, petiolate, estipulate but an axillary bud often producing a clasping, broadly reniform leaf (pseudostipule); blade entire or 3 to 7-lobed, often cordate, palmately or pinnately veined, variable. Flowers axillary, solitary, perfect, epigynous, zygomorphic. Calyx gamosepalous, variously inflated, thence more or less contracted, expanding into a 1- to 3-lobed limb. Corolla absent. Stamens typically 6, the anthers sessile and adnate to the style, 2-celled, dehiscing longitudinally. Ovary inferior, 6-loculate; placentation axile, the ovules numerous, anatropous. Styles 6, marginally connate, fleshy, with coroniform stigmatic lobes, or essentially capitate. Fruit a capsule, septicidally or septifragally 6-valved, often dehiscing acropetally. Seeds numerous, horizontally compressed in vertical rows, the embryo rudimentary in abundant endosperm.

In the treatment of *Aristolochia* presented here, it has seemed the wisest choice to include, in addition to the species collected in Panama, accounts of those reasonably certain to be found there. Accordingly, these species will be found incorporated into the key to species and described with the presently known groups in the formal treatment.

Perhaps a word of caution might be of some help when attempting to key flowering material in this genus. Many of the collections of the large-flowered species are collections of buds, and dimensions derived from them must be regarded as approximate. For example, the flowers of *Aristolochia grandiflora* become fourteen feet long but few collections reflect this great dimension. The buds undoubtedly develop for weeks before anthesis and few collectors are willing to return to the same location repeatedly for the sake of a single bloom; hence the measured length of the calyx tube as collected may be considerably less than the mature size.

a. Shrubs or low perennial herbs; pseudostipules absent.
  b. Stems glabrous; flowers axillary near the apices of young vegetative shoots; leaves cordate-reniform; perennial herbs with swollen roots. 1. A. NUMMULARIFOLIA
  bb. Stems woolly; flowers borne in clusters near the ground, cauliflorous; leaves extremely variable in size and shape; shrubs; capsules dehiscing apically .... 2. A. PANAMENSIS
aa. Lianas; stems hirsute to glabrous; flowers axillary or racemose on young shoots or if on old wood not produced near the ground; capsules dehiscing acropetally.
  c. Pseudostipules present.
    d. Leaves (other than pseudostipules) trilobate, the base truncate; calyx limb bilobate, the lower lobe ending in a filiform extension 8 to 20 cm. long .... 3. A. TRILOBATA
    dd. Leaves unlobed, the base cordate to subhastate.
      e. Flowers solitary, axillary, more than 8 cm. long, the axis of the calyx tube abruptly bent at the union of the utricle and the tube; ovary with a sharp bend at the distal end, thus bearing the flower to one side; leaves irregular, but with a tendency toward a cordate-hastate base, the lobes broad and circular in outline .... 4. A. ODORATISSIMA

ee. Flowers in axillary racemes, less than 6 cm. long, rectilinear; ovary without an apical bend; leaves simply cordate at the base.
f. Calyx limb strongly monolobate becoming broadly expanded with a plicature along its median nerve; utricle ovoid, gibbous, narrowing abruptly to the 5 mm.-long tube. 5. A. INFLATA
ff. Calyx limb unequally bilobate, the upper short and barely extended beyond the throat, the lower long, spatulate and non-plicate; utricle cylindric to spheroid, gradually and slightly narrowing to the 15 mm.-long tube. 6. A. ANGUICIDA
cc. Pseudostipules absent.
g. Ovary immediately subtended by a foliaceous bracteole.
h. Calyx tube glabrate, ca. 3 dm. long, yellow blotched with purple; bracteole orbicular. 7. A. ARBORESCENS
hh. Calyx tube densely pubescent at maturity, at anthesis ca. 3 m. long, white and pink blotched with purple; bracteole acuminate. 8. A. GRANDIFLORA
gg. Ovary not subtended by a foliaceous bracteole, the pedicels naked.
i. Calyx limb with numerous fimbriae on the inner surface. 9. A. COSTARICENSIS
ii. Calyx limb without fimbriae.
j. Leaves cordate-ovate, nearly as wide as long; stems glabrous.
k. Flowers borne in short racemes or clusters on old wood, cauliflorous.
l. Veins in leaves conspicuously marked with white borders; leaves long-acuminate; flowers small, 3 to 4 cm. long. 10. A. VERAGUENSIS
ll. Veins in leaves green; leaves short-acuminate; flowers longer than 20 cm., showy. 11. A. SYLVICOLA
kk. Flowers borne in many flowered racemes in axils of leaves of young shoots. 6. A. ANGUICIDA
jj. Leaves oblong, more than three times longer than wide.
m. Flowers rectilinear, more than 10 cm. long; leaves deeply cordate. 12. A. CHAPMANIANA
mm. Flowers with tube and limb reflexed on the utricle, ca. 5 cm. long; leaves truncate to subcordate at the base. 13. A. MAXIMA

1. ARISTOLOCHIA NUMMULARIFOLIA HBK. Nov. Gen. & Spec. 2:115. *t. 110.* 1817.

Aristolochia clausseni Duch. in Ann. Sc. Nat. ser. 4. 2:57. 1854.
Aristolochia emarginata Willd. ex Duch. in DC. Prod. 15–1:466. 1864.
Aristolochia pusilla Pohl, ex Duch. loc. cit. 1864.
Aristolochia tenera Pohl, ex Duch. loc. cit. 1864.
Aristolochia subclausa Wats. in Proc. Amer. Acad. 20:372. 1882.
Aristolochia pyrinea Taub. in Engl. Bot. Jahrb. 21:426. 1896.
Aristolochia exigua Lindm. in Bull. Herb. Boiss. ser. 2. 1:525. 1901.

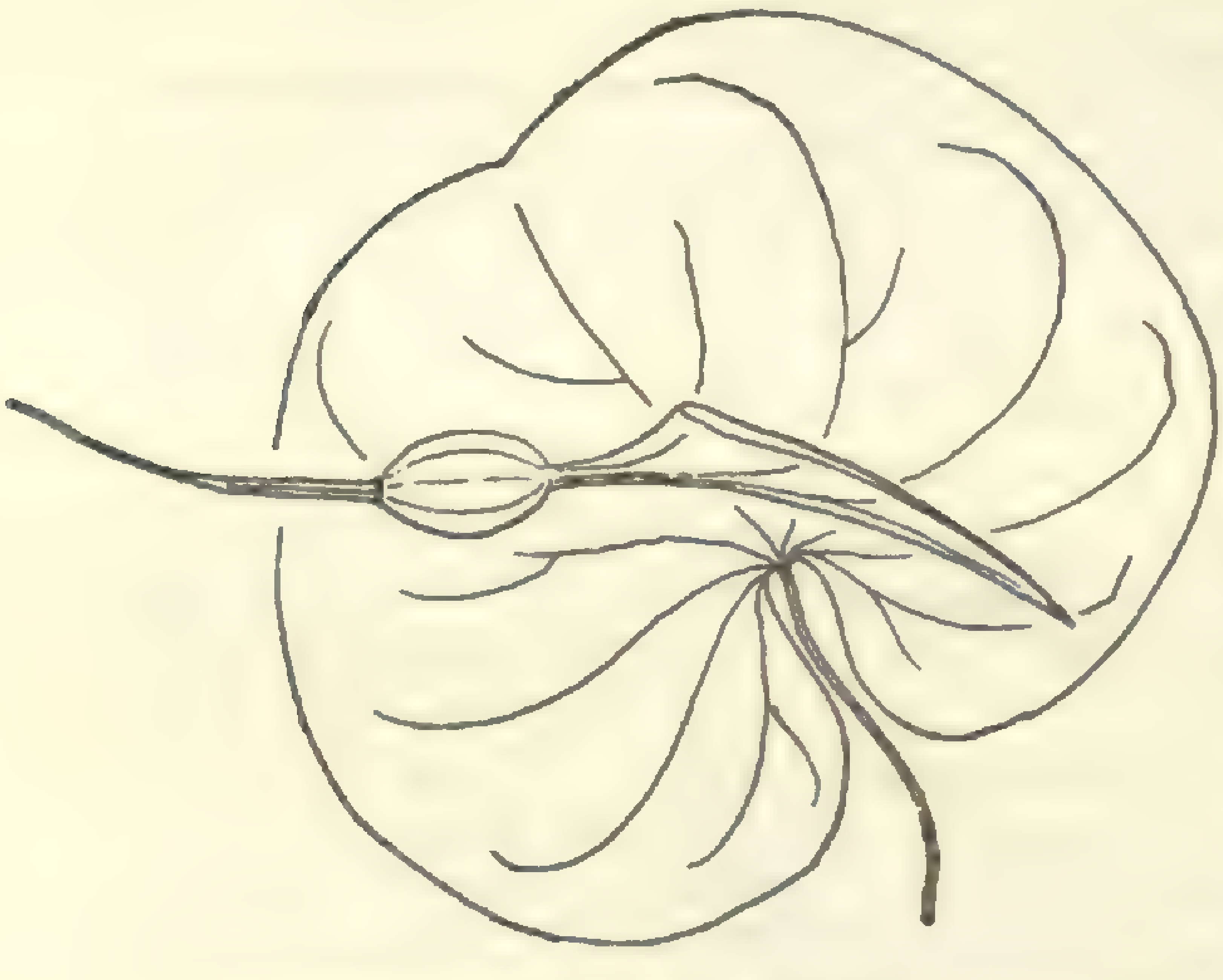
Fig. 90. *Aristolochia nummularifolia*

Herbs, 3 to 6 dm. tall, perennial, with thickened fusiform roots. Leaves alternate, somewhat distichous, reniform to acute and cordate, ca. 3 cm. broad, 2 to 3 cm. long, glabrous. Pseudostipules absent. Flowers small, axillary, rectilinear, the utricle, tube and monolobate limb nearly indistinguishable as such, ca. 2 to 4 cm. long, greenish yellow. Fruit cylindric, ca. 2 cm. long, 1 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 2 mm. wide, 0.2 mm. thick.

Columbia and Venezuela. To be sought in Panama.

2. ARISTOLOCHIA PANAMENSIS Standley, in Journ. Wash. Acad. Sci. 15:5. 1925.

Decumbent subshrubs, to 6 dm. tall. Leaves alternate, spiral, very variable in shape, narrowly lanceolate to broadly obovate, villous-tomentose, 5 to 15 cm. long, 3 to 10 cm. wide. Pseudostipules absent. Flowers cauliflorous, borne near the soil in inconspicuous short racemes, ca. 5 cm. long along the curved axis, brownish marked with purple, the utricle narrow, thence widening into a gibbous sac, the limb sharply reflexed on the utricle, the tube reduced to a constriction of the utricle. Gynostemium of 6 closely connate styles, capitate. Fruit cylindric, ca. 3 cm. long, 1 cm. wide, dehiscing apically. Seeds several, pyramidal, grooved, ca. 4 mm. wide.

Known only from Panama.

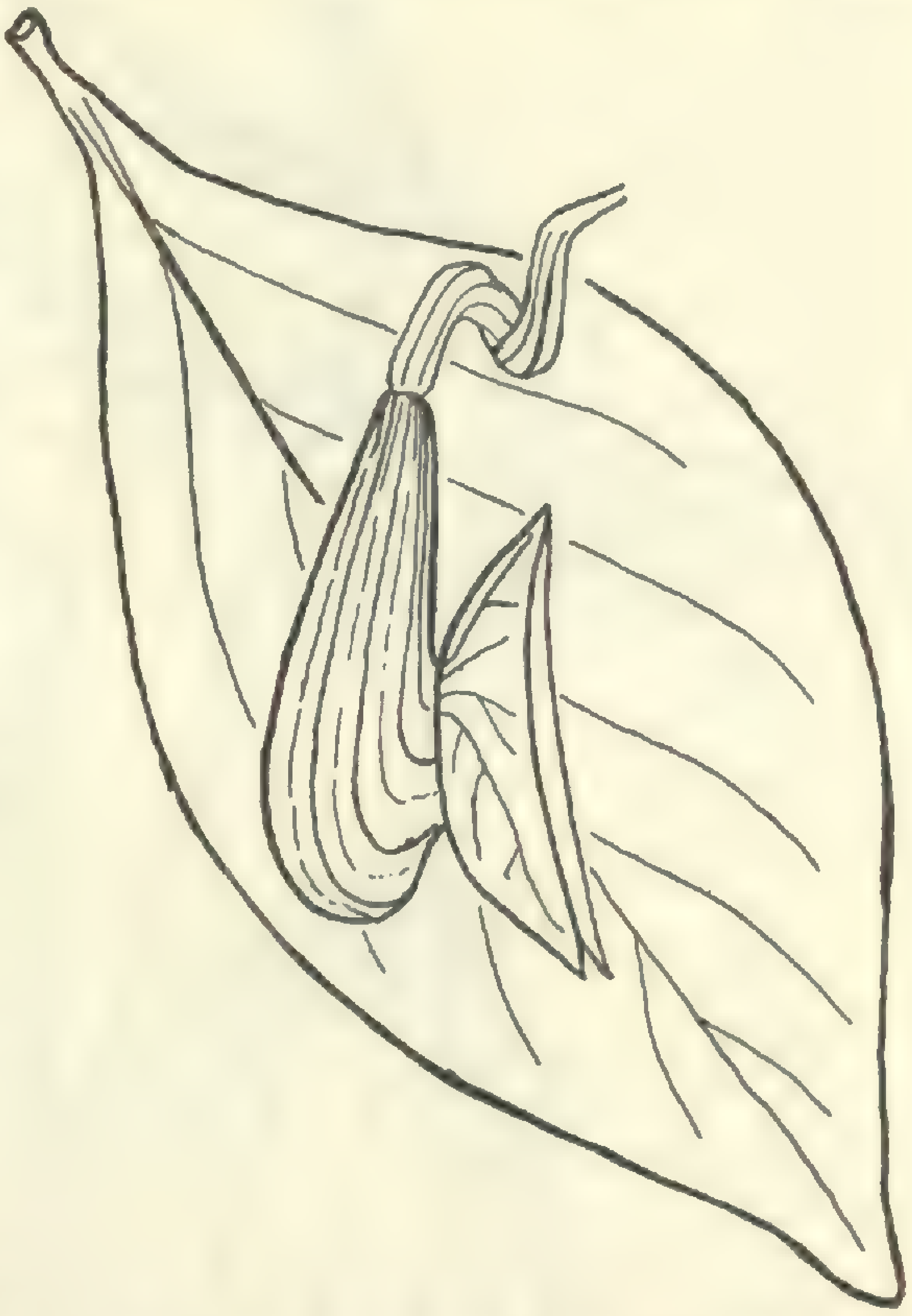

Fig. 91. *Aristolochia panamensis*

CANAL ZONE: Cocoa Plantation, *Lindsay 488*; Las Cascadas Plantation, near Summit, *Standley 29515, 25740*; Río Paraíso, above East Paraíso, *Standley 29906* (type); Río Pedro Miguel, near East Paraíso, *Standley 29950*. CHIRIQUÍ: Pastures and forested river banks east of Gualaca, alt. 500 ft., *Allen 5040*; vicinity of San Félix, eastern Chiriquí, alt. 0-120 m., *Pittier 5463*; San Félix, eastern Chiriquí, *Pittier 5750*.

3. ARISTOLOCHIA TRILOBATA L. Sp. Pl. ed. 1. 2:960. 1753.

Aristolochia trifida Lamk. Encyc. 1:251. 1783.
Aristolochia triloba Salisb. Prod. 214. 1796.
Aristolochia macroura Gomez, in Mem. Ac. Lisboa 3:77. 1812.
Aristolochia caracasana Spreng. Syst. 3:753. 1826.
Aristolochia appendiculata Vell. Fl. Flum. 9: *t. 98*. 1827.
Aristolochia caudata Booth, ex Lindl. in Bot. Reg. *t. 1453*. 1831.
Aristolochia tapetotricha Lem. Illustr. Hort. 3:misc. 22. 1856.
Howardia trifida Klotzsch, in Monatsb. Acad. Berl. 1859:617. 1859.
Howardia trilobata Klotzsch, loc. cit. 1859.
Howardia macroura Klotzsch, loc. cit. 1859.

Twining, glabrous lianas. Leaves alternate, spiral, subpalmate, 3-lobate, truncate at the base, glabrous, ca. 6 cm. wide, 6 cm. long. Pseudostipules present. Flowers axillary, ca. 15 to 20 cm. long, red-brown with purple stripes, the utricle elliptic, ca. 5 cm. long, 3 cm. wide, curving abruptly at the apex with slight narrowing into the tube, ca. 5 cm. long, 2 to 3 cm. wide, ending in the bialate limb which terminates in a long filiform extension. Seeds numerous, horizontally compressed, 6 mm. diameter, 0.75 mm. thick.

Throughout tropic Central and South America.

Fig. 92. *Aristolochia trilobata*

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1404, 1812.* CANAL ZONE: Chagres, Isthmus of Panama, *Fendler 445, 440.*

4. ARISTOLOCHIA ODORATISSIMA L. Sp. Pl. ed. 2. 2:1362. 1763. non Benth., nec Vell.

Aristolochia moschata Wedd. ex Duch. in DC. Prod. 15–1:475. 1864.
Aristolochia odoratissima β grandiflora Duch. loc. cit. 1864.
Aristolochia martiniana Standl. in Publ. Field Mus. Bot. 17:238. 1937.

Lianas, twining, scandent, glabrous. Leaves alternate, variable cordate-hastate to sub-trilobate, membranous, ca. 15 cm. long, 12 cm. wide. Pseudostipules present. Flowers axillary, the calyx borne at an abrupt angle at the apex of the ovary, dark red, mottled and striped with lighter shades of red and yellow, the utricle ovate, 2 to 3.5 cm. long, the tube arising at a right angle from the side of the utricle, 15 to 20 mm. long, the limb thick, delicate, crenate, suborbiculate, 6 to 12 cm. diameter. Fruit cylindric to subfusiform, abruptly bent in a right angle at the apex, slightly curved, 1.5 cm. diameter, 4 cm. long, dehiscing acropetally. Seeds numerous, horizontally compressed, 5 mm. diameter, 0.5 mm. thick.

Southern Central America, northwestern South America, Amazonia.

Fig. 93. *Aristolochia odoratissima*

BOCAS DEL TORO: Changuinola Valley, *Dunlap 556*; vicinity of Chiriquí Lagoon, Bastimentos, Mariano Creek, *von Wedel 2903*; vicinity of Chiriquí, Old Bank Island, *von Wedel 2046*; vicinity of Chiriquí Lagoon, Water Valley, *von Wedel 1556*; vicinity of Chiriquí Lagoon, *von Wedel 1200*; Water Valley, *von Wedel 791*.

5. ARISTOLOCHIA INFLATA HBK. Nov. Gen. & Spec. 2:145. 1817.

Aristolochia gibbosa Duch. in Ann. Sc. Nat. Ser. 4–2:53. 1854.
Howardia benthamii Klotzsch, in Monatsb. Acad. Berl. 1859:620. 1859.

Slender, scandent lianas. Leaves alternate, ovate, acute, cordate, 3 to 5 nerved, membranous, ca. 10 cm. long, 8 cm. wide, glabrous. Pseudostipules present. Flowers solitary, axillary, rectilinear, borne on young leafy shoots, 4 to 6 cm. long, yellow spotted purple, the utricle ovoid, 1 to 1.5 cm. long, narrowing obliquely to a short tube 7.5 mm. long, acuminate. Fruit cylindric, ca. 3.5 cm. long, 1 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 2 mm. diameter, 0.5 mm. thick.

Central America.

CANAL ZONE: Camino de Corozal, *Bro. Heriberto 247*. COCLÉ: between Aguadulce and the Chico R., alt. 20 m., *Pittier 5008*; Penonomé and vicinity, alt. 50–1000 ft., *Williams 204*. HERRERA: vicinity of Chitré, alt. 20 m., *Allen 1101*. PANAMÁ: vicinity of Pacora, alt. 35 m., *Allen 2032*; Argicultural Experiment Station at Matías Hernández, *Pittier 6872*; along the Corozal Road, near Panamá, *Standley 26770*; vicinity of Juan Franco Race Track, near Panamá, *Standley 27796*; near Punta Paitilla, *Standley 26246*; Taboga Island, *Standley 27029, 27963*; Tumba Muerto Road, near Panamá, *Standley 29796*; sabanas, north of Panamá City. *Bro. Paul 587*; Panamá, *Hayes 781, 294, 146*.

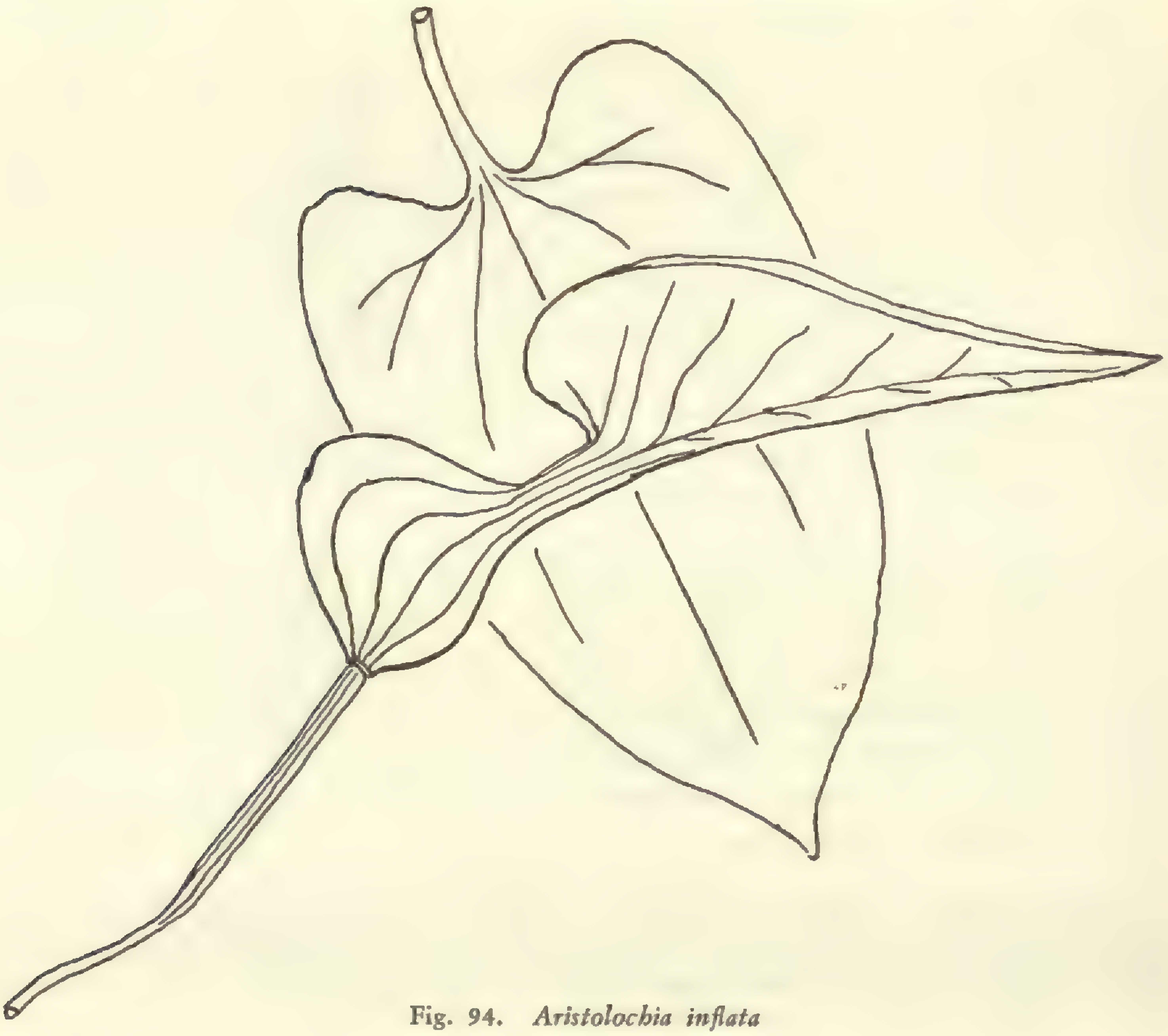

Fig. 94. *Aristolochia inflata*

6. ARISTOLOCHIA ANGUICIDA L. Sp. Pl. ed. 2. 2:1362. 1763.

Aristolochia loriflora Mast. in Engl. Bot. Jahrb. 8:220. 1887.
Howardia anguicida Klotzsch, in Monatsb. Acad. Berl. 1859:611. 1859.

Fig. 95. *Aristolochia anguicida*

Lianas, with slender stems. Leaves alternate, spiral, oblong-ovate, cordate, 7 to 10 cm. broad, 10 to 15 cm. long, glabrous. Pseudostipules usually present. Flowers axillary, rectilinear, ca. 2.0 to 2.5 cm. long, mottled purple, the utricle gibbous, 0.9 cm. long, narrowing abruptly into the tube, ca. 1.0 cm. long, which widens gradually into a funnelform, unequally monolobate limb. Fruit cylindric, 3 cm. long, 1.5 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 0.4 cm. diameter, 1 mm. thick.

Honduras, Guatemala and south to Venezuela and Colombia. To be sought in Panama.

Fig. 96. *Aristolochia arborescens*

7. Aristolochia arborescens Linn. Sp. Pl. 960. 1753.

Aristolochia foetens Lindl. Bot. Reg. *t. 1824.* 1836.
Howardia foetens Klotzsch, in Monatsb. Acad. Berl. 1859:610. 1859.

Lianas, with twining stems. Leaves alternate, cordate, apex acute to acuminate, membranous, 5 to 20 cm. broad, 8 to 30 cm. long, glabriusculus at maturity. Pseudostipules absent. Flowers immediately subtended by an orbiculate, perfoliate bracteole, axillary, solitary but occasionally in pairs, glabrescent, yellow, blotched with purple, the utricle broadly gibbous-clavate, ca. 30 cm. long, the tube sharply reflexed on the utricle, ca. 35 cm. long, widening into a throat distinguished by peculiar annular venation and constriction, ca. 5 cm. long, the limb obliquely funnelform, terminating in a struppate extension ca. 20 cm. long; the odor putrid. Fruit ovate-cylindric, ca. 10 cm. long, 6 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 1 cm. diameter, 2 mm. thick.

Mexico south to Colombia.

colón: Fató (Nombre de Dios), sea level, *Pittier 4145*. darién: vicinity Pinogana, alt. 20 m., *Allen 4292*; trail between Pinogana and Yavisa, alt. 15 m., *Allen 291*.

8. Aristolochia grandiflora Sw. Prod. Veg. Ind. Occ. 3:1566. 1806, non Gomez, nec Arruda, nec Vahl.

Aristolochia gigas Lindl. Bot. Reg. *t. 60*. 1842.
Howardia grandiflora Klotzsch, in Monatsb. Acad. Berl. 1859:610. 1859.
Aristolochia grandiflora β hookeri Duch. in DC. Prod. 15–1:473. 1864.

Twining lianas, older stems ridged with cork. Leaves alternate, cordate, apex acute to acuminate, membranous, 5 to 20 cm. broad, 7 to 30 cm. long, densely pilose to velutinous becoming nearly glabrous on upper surface. Pseudostipules absent. Flowers immediately subtended by an acuminate foliaceous bracteole, borne on young stems, axillary, solitary, ca. 3 m. long, the color white blotched with purple, pilose, the utricle broadly gibbous-clavate, ca. 45 cm. long, the tube sharply reflexed on the utricle, ca. 40 cm. long, the limb obliquely salverform, terminating in a filiform extension from the medial lower edge, the odor of "old tobacco". Fruit ovate-cylindric, 10 cm. long, 4 to 6 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 1 cm. diameter, 3 mm. thick.

Panama, south throughout Amazonia.

darién: vicinity of Yape, alt. 30 m., *Allen 647*.

This species rarely is collected. It appears that practically all of the large-flowered Aristolochia collections have been named *grandiflora,* but are properly *A. arborescens.* There is a relatively sharp distinction between the two species. *A. grandiflora* has truly a huge flower, perhaps the largest in American tropics, a total reported axial length in excess of 4.5 meters, while *A. arborescens* is about one-fourth as large. The flowers of the former are velutinous without and differ in color and odor from the latter. *A. arborescens* has a well-differentiated throat, while *A. grandiflora* is not markedly endowed with this feature.

9. Aristolochia costaricensis (Klotzsch) Duch. in DC. Prod. 15–1:450. 1864.

Howardia costaricensis Klotzsch in Monatsb. Acad. Berl. 1859:614. 1859.
Aristolochia ferruginea T. S. Brandeg. in Univ. Calif. Publ. Bot. 6:51. 1914.
Aristolochia haughtiana Hoehne, in Arquiv. Bot. Estad. S. Paulo 2:99. 1947.

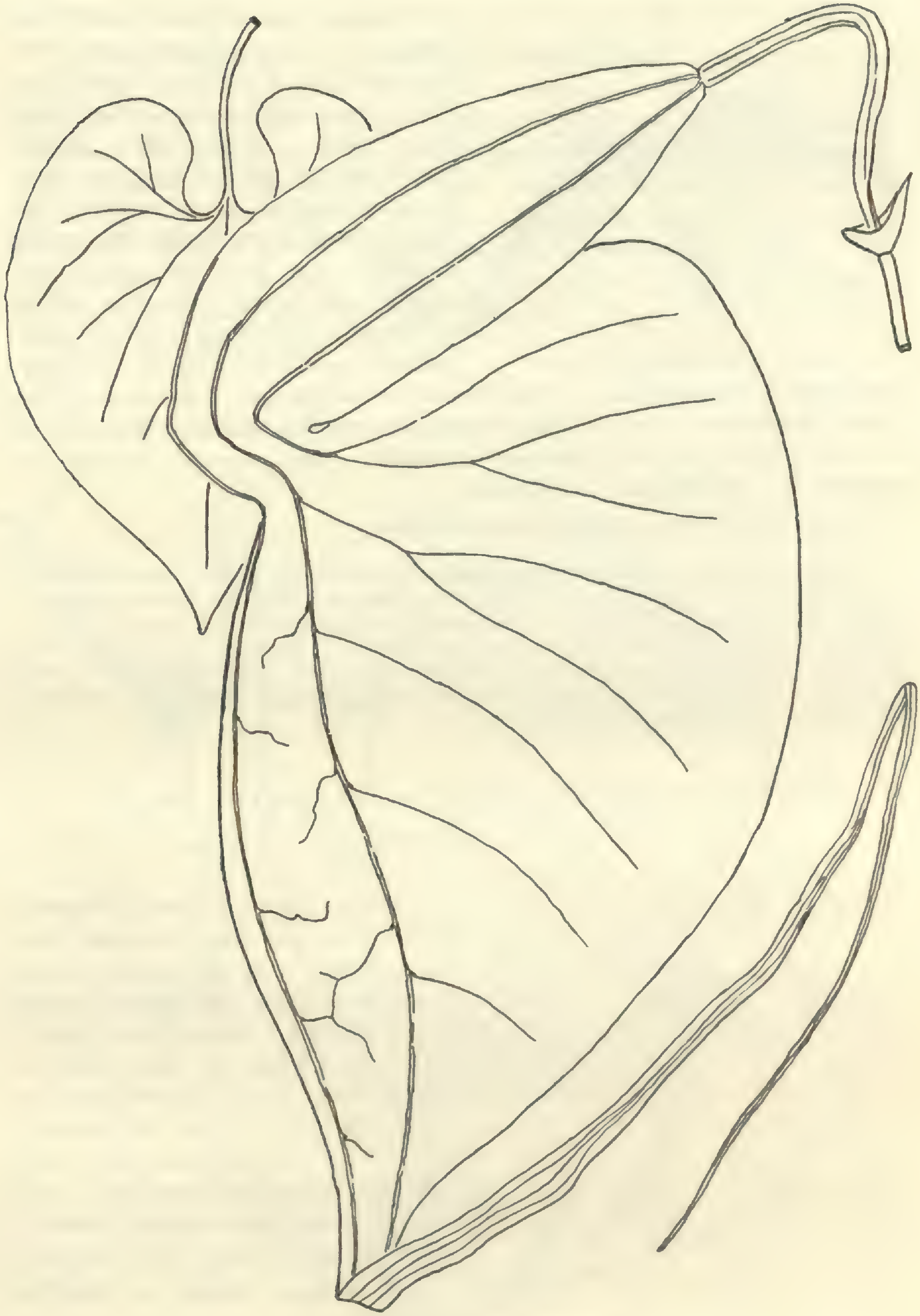

Fig. 97. *Aristolochia grandiflora*

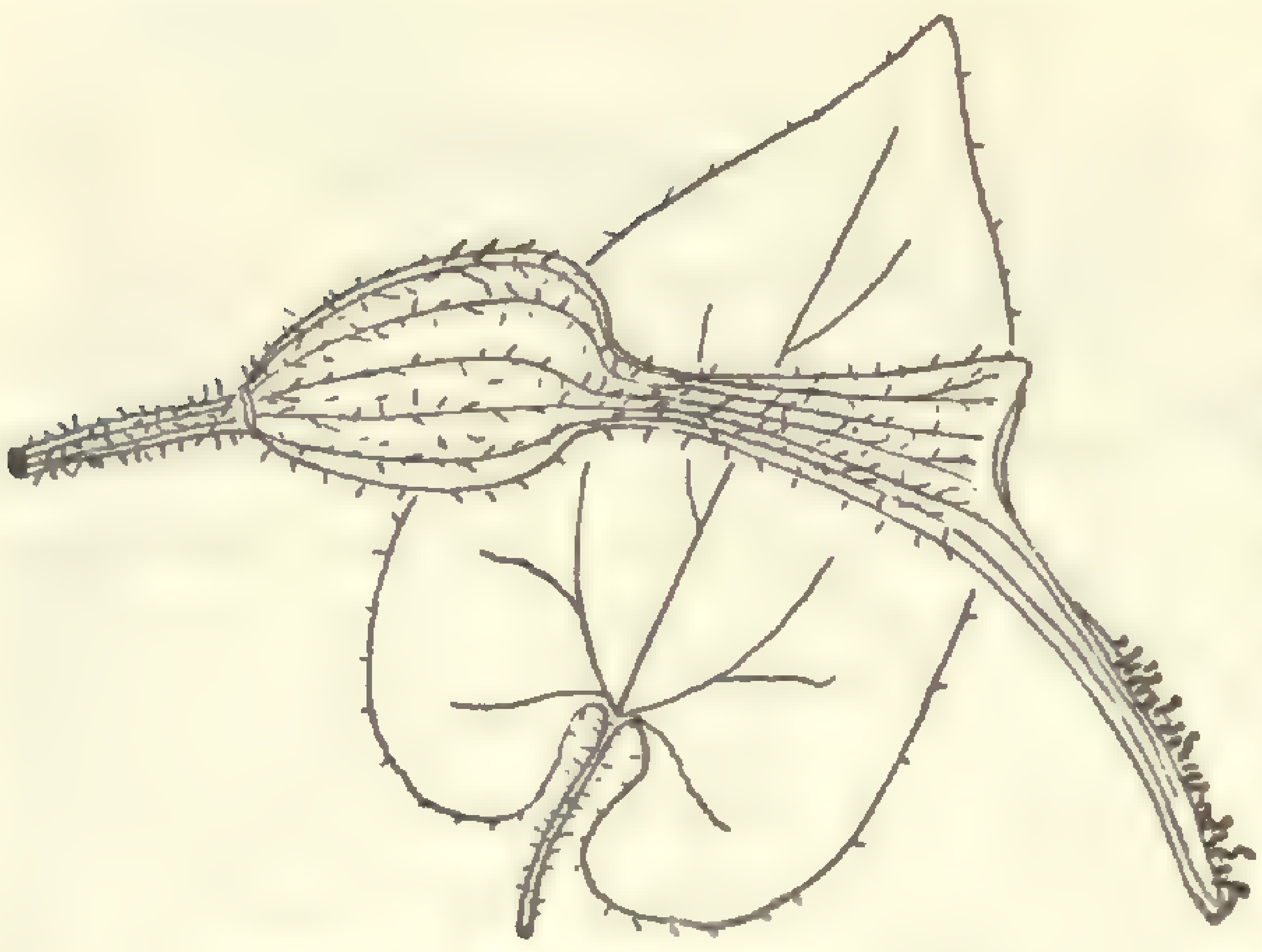

Fig. 98. *Aristolochia costaricensis*

Twining, scandent lianas, hispid-pilose throughout. Leaves alternate, spiral, cordate, apex acute, 9 to 15 cm. broad, 10 to 25 cm. long, upper surface glabrescent, lower pilose. Pseudostipules absent. Flowers axillary, solitary, ca. 7 cm. long, the color brownish-purple marbled with white, densely pilose-hispid, the utricle ellipsoid, 3 cm. long, the tube arising obliquely and abruptly from the side of the utricle near the distal end, 2 cm. long, gradually enlarging into the obliquely funnelform limb which bears a linguiform lobe variously spotted and mottled and covered on the inner side with many fleshy excrescenses or fimbriae. Fruit ovoid, ca. 6 cm. long, 4 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 1 cm. diameter, 2 mm. thick.

Tropic Central and northern South America.

CANAL ZONE: Barro Colorado Island, *Aviles 70*; Gatún, *Hayes 620*; around Gamboa, alt. 40–80 m., *Pittier 4431*; Barro Colorado Island, *Shattuck 164, 726*. BOCAS DEL TORO: Bank of Changuinola R., *Dunlap 420;* Changuinola Valley, *Dunlap 18*; vicinity of Chiriquí Lagoon, *von Wedel 1228, 1267*. DARIÉN: vicinity of Yape, alt. 30 m., *Allen 864*. PANAMÁ: Alhajuela, Chagres Valley, alt. 30–100 m., *Pittier 2326*; Mamoni R., above Chepo, alt. 23–25 m., *Pittier 4732*; north of Panamá City, *Bro. Paul 374*. PROVINCE UNKNOWN: western Panama, *Stork 18*.

10. ARISTOLOCHIA VERAGUENSIS Duch. in DC. Prod. 15–1:458. 1864.

Howardia veraguensis Klotzsch, ex Duch. loc. cit. 1864.

Twining lianas. Leaves alternate, spiral, ovate, apex long acuminate, base deeply cordate, 12 to 20 cm. broad, 15 to 30 cm. long, veins and adjacent tissues white, glabrous. Pseudostipules absent. Flowers cauliflorous in short racemose clusters, small, purple, red-reticulate, the utricle subspheric, ca. 1 cm. long, narrowing into the 1.5 cm. long tube which unequally enlarges to form the 2 cm. long mucronate limb, which is arcuately reflexed upon the utricle. Fruit not seen.

East Panama, south to Brazilian Amazonia.

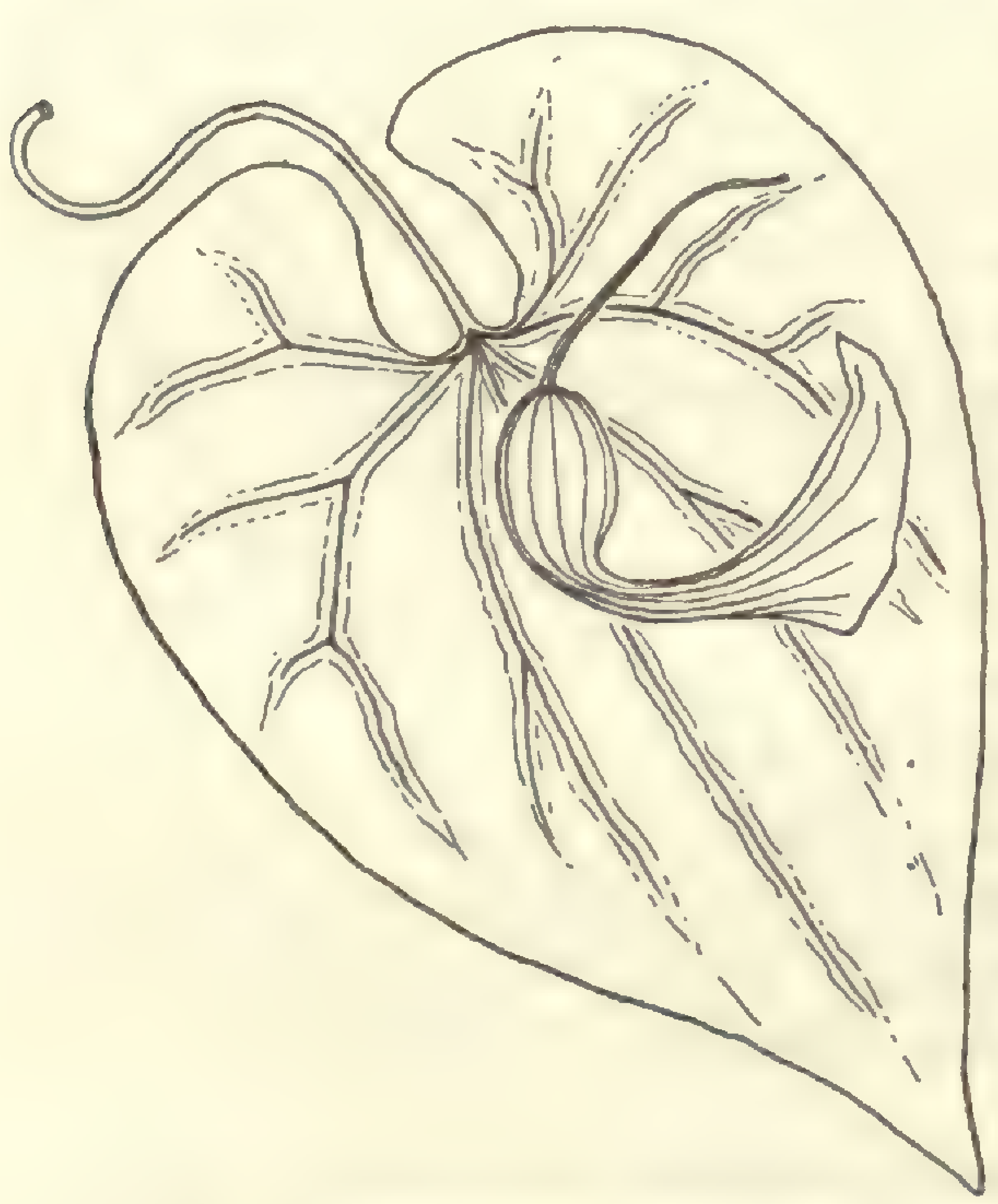

Fig. 99. *Aristolochia veraguensis*

DARIÉN: El Reál, *Allen 2210*.

11. Aristolochia sylvicola Standl. Journ. Wash. Acad. Sci. 15:5–6. 1925.

Slender, scandent lianas. Leaves broadly rounded-deltoid, acuminate or acute, the base very shallowly cordate to truncate, 8 to 12 cm. broad, 10 to 20 cm. long, dark green and glabrous above, beneath light green to white, subarachnoid-velutinous to thinly puberulent. Pseudostipules absent. Flowers cauliflorous in short, few-flowered racemes, maroon finely marbled with white and pink, the utricle ellipsoid, 6 cm. long, the tube short and reflexed, thence opening into the showy limb which is notched at the upper medial edge, ca. 20 cm. wide. Fruit long-cylindric, 12.5 cm. long, 3 cm. wide, dehiscing acropetally. Seeds numerous, revolute, 3 mm. diameter, 8 mm. long, 2 mm. thick.

Known only from Panama.

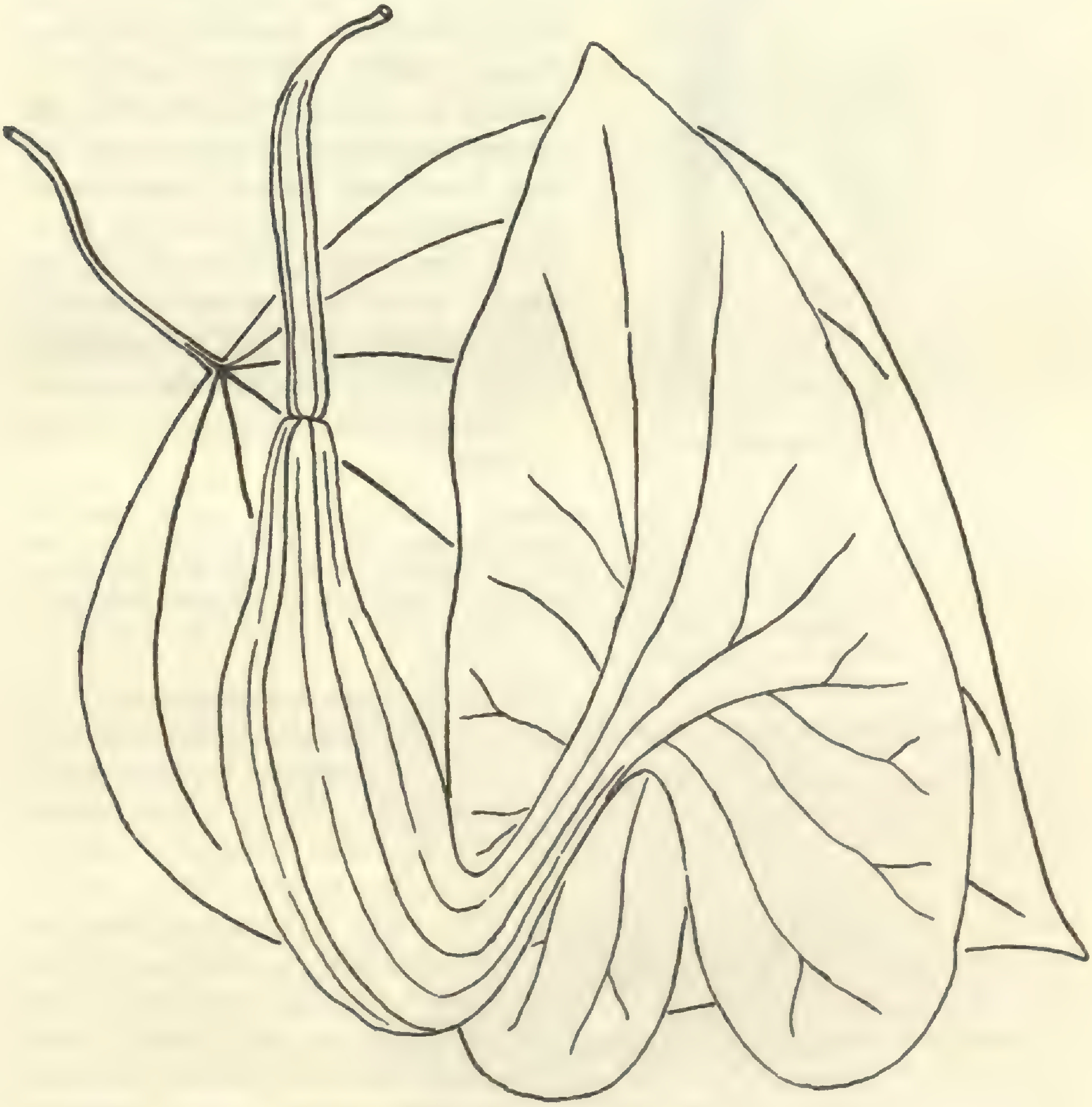

Fig. 100. *Aristolochia sylvicola*

BOCAS DEL TORO: Changuinola Valley, *Dunlap 247*. CANAL ZONE: Summit, *Allen 2250*; Barro Colorado Island, *Shattuck 640*; Barro Colorado Island, alt. 120 m. or less, *Standley 40866*; hills north of Frijoles, *Standley 27469* (type); Barro Colorado Island, alt. 900 m., *Wetmore & Abbe 1*. DARIÉN: Trail between Paya and Palo de las Letras, *Stern et al. 204*.

12. ARISTOLOCHIA CHAPMANIANA Standl. in Contrib. Arn. Arb. 5:60. 1933.

Aristolochia maxima var. *cordata* Standl. in Field Mus. Publ. Bot. 8:136. 1930.

Twining, scandent lianas, sparsely hispidulous-pubescent. Leaves alternate, subdistichous, oblong-spatulate, apex acute to obtuse, base typically deeply cordate, 3 to 6 cm. broad, 10 to 20 cm. long, glabrescent. Pseudostipules absent. Flowers solitary, axillary, rectilinear or slightly arched, dark purple-brown, the utricle long-ellipsoid, ca. 5 cm. long, the tube 3 cm. long, splitting monolaterally into the oblong-lanceolate limb, ca. 7 cm. long. Fruit ovate-cylindric, ca. 12 cm. long, 5 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 1 cm. diameter, 2 mm. thick.

Central America and northern South America.

Fig. 101. *Aristolochia chapmaniana*

CANAL ZONE: Barro Colorado Island, *Bangham 455*; Cerro Gordo, near Culebra, alt. 50–290 m., *Pittier 2304*; Barro Colorado Island, *Shattuck 413* (type); Barro Colorado Island, *Shattuck 1076*; Barbour-Lathrop Trail, alt. 900 m., *Wetmore & Woodworth 77*; Barro Colorado Island, *Zetek 3618*. COCLÉ: between Las Margaritas and El Valle, *Woodson et al. 1739*; above Penonomé, alt. 2000–3000 ft., *Williams 548*. PANAMÁ: San José Island, *Erlanson 424*; San José Island, *Johnston 726, 1253, 1316*.

13. ARISTOLOCHIA MAXIMA L. Spec. Pl. ed. 2. 2:1361. 1763.

Aristolochia geminiflora HBK. Nov. Gen. & Spec. 2:118. *t. 117*. 1817.
Aristolochia reticulata Seem. Bot. Voy. Herald, 193. 1854.
Howardia geminiflora Klotzsch, in Monatsb. Acad. Berl. 1859:619. 1859.
Howardia gollmerii Klotzsch, loc. cit. 1859.
Howardia hoffmanni Klotzsch, loc. cit. 621. 1859.
Howardia maxima Klotzsch, loc. cit. 615. 1859.
Aristolochia biflora Willd. ex Duch. in DC. Prod. 15–1:457. 1864.
Aristolochia mathewsii Duch. loc. cit. 497. 1864.
Aristolochia maxima α maxima Duch. loc. cit. 456. 1864.
Aristolochia maxima β geminiflora Duch. loc. cit. 457. 1864.
Aristolochia maxima γ angustifolia Duch. loc. cit. 1864.
Aristolochia reticulata J. F. Holton, ex Duch. loc. cit. 1864.
Aristolochia sprucei Mast. in Mart. Fl. Bras. 4–2:88. 1875.
Aristolochia asperifolia Ule, in Verh. Bot. Ver. Prov. Brandenb. 47:121. 1905.

Twining, scandent lianas. Leaves alternate, spiral, oblong-spatulate, apex acute to obtuse, sometimes minutely mucronate, base truncate to shallowly subcordate, 4 to 8 cm. broad, 10 to 20 cm. long, glabrous. Pseudostipules absent. Flowers in clustered racemes with reduced leaves, purple-brown, the utricle ovoid, ca. 3 cm. long, narrowing abruptly into the recurved tube, ca. 1 cm. long, which gradually widens into the strongly reflexed limb, ca. 3 cm. long. Fruit ovate-cylindric, ca. 15 cm. long, 7 cm. wide, dehiscing acropetally. Seeds numerous, horizontally compressed, 1.2 cm. diameter, 3 mm. thick.

Central America and tropic South America.

PANAMÁ: between Las Sabanas and Matías Hernández, *Standley 31839*; Taboga Island, *Standley 27090, 27856*; Tumba Muerto Rd., near Panamá, *Standley 29804*; sabanas, north of Panamá City, *Bro Paul 517*; Belleviota, *Macbride 2763*.

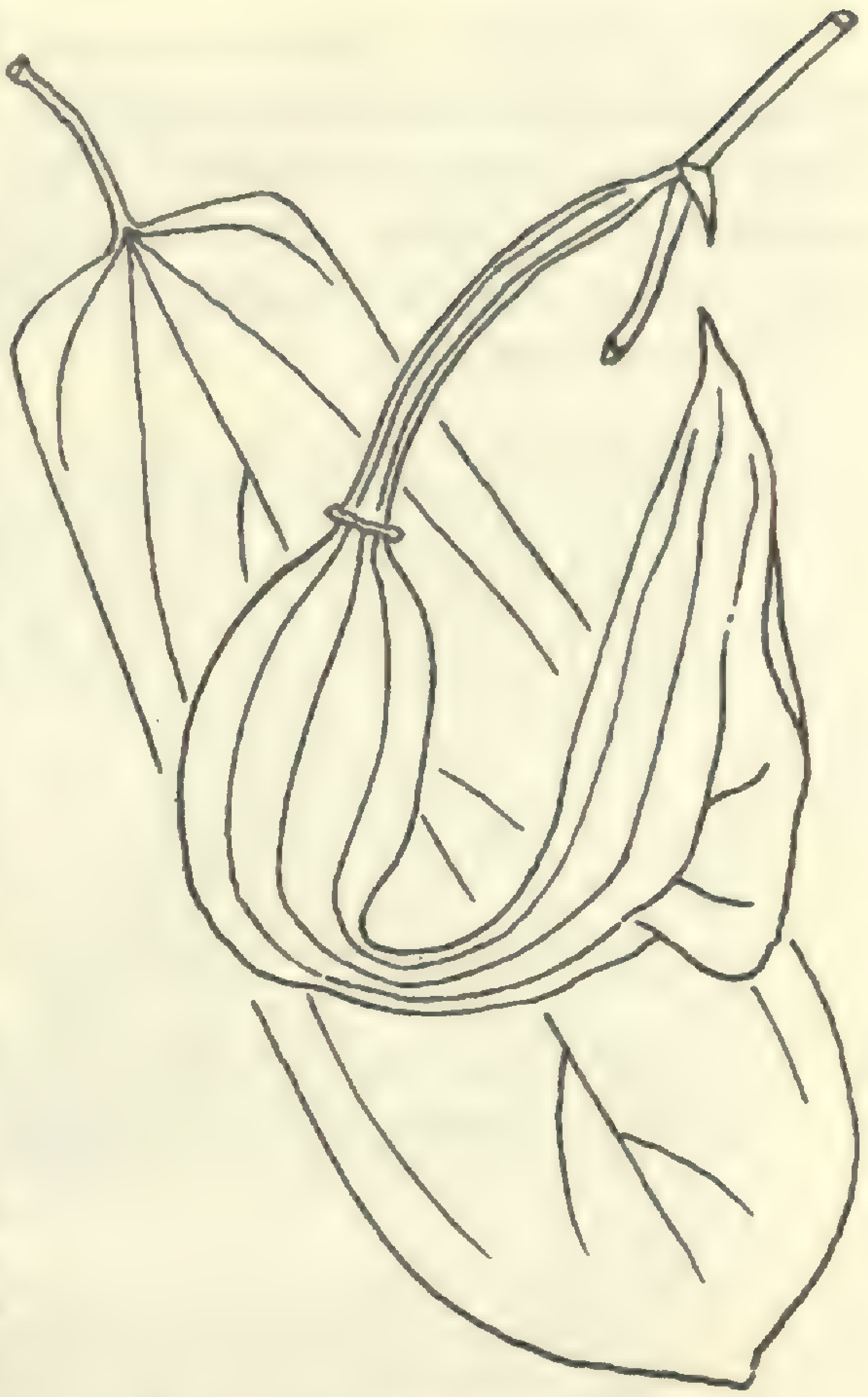

Fig. 102. *Aristolochia maxima*

POLYGONACEAE

By JAMES A. DUKE

Flowers perfect or unisexual, monoecious or dioecious, trimerous or dimerous, on short usually articulate pedicels, solitary or fasciculate within scariose ochreolae. Calyx uniseriate or biseriate, hypogynous, of 3–6 free or partially connate tepals. greenish to red or white. Stamens usually 6–9, rarely more or less, the filaments filiform or flattened, occasionally partially adnate to the calyx; anthers 2- or 4-locular, usually versatile and introrse. Ovary superior, triquetrous or lenticular, unilocular, containing a single erect orthotropous ovule, the stigmata filiform or capitate and entire or variously fringed. Achene trigonous or lenticular, usually with a crustaceous pericarp, the embryo usually excentric in a mealy endosperm. Herbs, shrubs, trees or vines with alternate usually entire simple leaves with ochreate stipules, the stems often sulcate, hollow and geniculate. Flowers in terminal racemes or panicles, often spicate, rarely cymose, or solitary or fasciculate in the axils, usually subtended by scariose ochreolae.

This predominantly north temperate family of about 30 genera and 700 species is represented in Panama by six genera. It is economically a rather unimportant family. *Fagopyrum,* the buckwheat, and *Rheum,* the rhubarb, are crops of limited importance. *Antigonon* spp., *Polygonum* spp. and *Muehlenbeckia* spp. are often cultivated in Central America as ornamentals. Some species of *Rumex* are troublesome lawn weeds.

a. Plants herbaceous or suffruticose (spp. of *Polygonum* § TINARIA twining); calyx of 3–6 tepals, the inner slightly larger; stamens 5–9.
  b. Calyx of 6 tepals, the outer reflexed or spreading, the inner usually larger and longitudinally folded, often tuberculate; flowers perfect or dioecious, verticillate; filaments shorter than the anthers .... 1. RUMEX
  bb. Calyx of 3–5 subequal tepals, not reflexed, closely conforming to the achene, not plicate or tuberculate; flowers perfect, not verticillate; filaments longer than the anthers .... 2. POLYGONUM
aa. Plants shrubby, arboreal or lianoid; calyx of 5–6 tepals, the outer slightly or greatly larger than the inner; stamens mostly 8–9.
  c. Achenes scarcely if at all exceeded by the tepals; tepals discrete and scariose or showing tendencies to form a fleshy calyx tube fused with the achene; tepals 5, the outer only slightly larger than the inner; stamens 8.
    d. Flowers perfect; tepals cordate, discrete, becoming scariose, loosely investing the achene; vines with tendrils .... 3. ANTIGONON
    dd. Flowers dioecious or polygamo-dioecious (perfect in *Muehlenbeckia* spp.); tepals not cordate, bony to fleshy but not scariose, closely investing the achene; trees, shrubs or scramblers without tendrils.
      e. Inflorescences both axillary and terminal, dioecious or perfect; tepals discrete nearly to their base; scramblers (in Panama), the twigs terete to quadrangulate, not lenticular .... 4. MUEHLENBECKIA
      ee. Inflorescences terminal on primary or short lateral branches, dioecious with staminodes or pistillodes developed; tepals forming a dry to fleshy tube, at least at their bases; trees in Panama (except one scrambler with bilateral wood and lenticular twigs). 5. COCCOLOBA
  cc. Achenes conspicuously exceeded by 3 wing-like outer tepals; outer tepals of the pistillate flowers basally fused to form a tube free of the achene; tepals 6, the outer much longer and broader than the inner in pistillate flowers; stamens 9 .... 6. TRIPLARIS

1. RUMEX L.

RUMEX L. Sp. Pl. 333. 1753.

Flowers perfect or unisexual, pedicellate, few to many in verticillate ochreolate fascicles. Perianth of 6 tepals, the outer 3 usually smaller and spreading or reflexed, the inner 3 cordate, entire or lacerate, frequently with an abaxial tubercle, usually accrescent and closely investing the achene. Stamens 6, discrete, the filaments usually shorter than the anthers, the anthers mostly 2-locular and loculicidal. Ovary trigonous with 3 spreading to reflexed filiform styles capped by fimbrillate peltate stigmata. Achene triquetrous, smooth and lustrous or rough and dull, usually included. Glabrous usually perennial herbs, occasionally becoming quite tall and shrubby. Leaves alternate, entire or rarely dentate, occasionally tending to form rosettes, the ochreae hyaline and rather tardily deciduous.

Of this large predominantly temperate genus, only two species, both probably naturalized from Europe, are thus far represented in the flora of Panama. Here they tend to be weeds in lawns and pastures at higher elevations. *R. costaricensis*

Fig. 103. *Rumex crispus*

Rechinger, a strikingly large species, is apparently endemic to the high mountains of Costa Rica. Three other species are reported in Guatemala by Standley & Steyermark (in Field Mus. Bot. 24^4:131. 1946).

a. Flowers perfect, the inner tepals tuberculate, 3.5–5 mm. long; achenes smooth, about 3 mm. long; leaves cordate to acute basally; plants non-clonal, with yellowish taproots .... 1. R. CRISPUS

aa. Flowers dioecious, the inner tepals not tuberculate, about 1 mm. long; achenes rough, about 1 mm. long; leaves hastate; plants clonal, with creeping rootstocks .... 2. R. ACETOSELLA

1. Rumex crispus L. Sp. Pl. 335. 1753.

Mostly unbranched coarse glabrous perennials with yellowish taproots. Leaves glabrous, lanceolate to oblong, apically acute, basally acute to cordate, the cauline blades mostly 10–12 cm. long by 0.5–3 cm. broad; petioles 1–5 cm. long; ochreae up to 2.5 cm. long, tardily deciduous. Inflorescences of crowded many-flowered ochreolate verticils in racemes or panicles. Flowers perfect, on pedicels mostly 5–12 mm. long; outer tepals oblong, 1–2 mm. long, scarcely accrescent; inner tepals broadly ovate to cordate, accrescent becoming 3.5–5 mm. long, 2–3.5 mm. broad, with a prominent exterior tubercule developing on 1 or 3 of them; stamens 6, discrete, the filaments mostly less than 0.5 mm. long, the anthers 1–1.5 mm. long, basifixed; ovary trigonous, the 3 styles usually reflexed, with 3 peltate fimbrillate stigmata. Achenes triquetrous, brown, lustrous, included, often capped by the persistent styles and stigmata, 2.5–3 mm. long, 2–2.5 mm. broad.

CHIRIQUÍ: Alto Lino, wayside roadside, 4200 ft., *Bro. Maurice 883*.

A native of Eurasia, this is a widespread weed, and common in temperate portions of the Americas. In Guatemala it is called *lengua de vaca* and *lengua de caballo*. The leaves are occasionally cooked as a potherb.

2. Rumex acetosella L. Sp. Pl. 538. 1753.

Acetosella acetosella (L.) Small, Man. SE. Fl. 446. 1933.

Low delicate glabrous perennials with slender creeping rootstocks. Leaves glabrous, lanceolate-hastate, apically acute to rounded, 1–3 cm. long, 3–8 mm. broad; petioles 1–5 cm. long; ochreae mostly 0.5–1 cm. long, tardily deciduous. Inflorescences of panicles of remote few-flowered verticils. Flowers dioecious, on pedicels mostly less than 3 mm. long; outer tepals oblong to narrowly ovate, about 0.5 mm. long, scarcely accrescent; inner tepals broadly ovate, about 1 mm. long, scarcely accrescent, not tuberculate; stamens 6 discrete, the filaments less than 0.3 mm. long, the anthers 0.5–1 mm. long, bilocular and loculicidal; ovary trigonous, the 3 styles spreading, with 3 peltate fimbrillate stigmata. Achene triquetrous, brown, dull and rough, often slightly exserted, about 1 mm. long.

CHIRIQUÍ: Cerro Punta, ca. 6025 ft., *P. White 196*; Valley of the upper Río Chiriquí Viejo, *P. White 60*.

This species, like the former, is a native of Eurasia now widespread in temperate regions of the Americas. In Costa Rica it is called *ruibarbillo*. Due to its persistent rootstocks, this is often an obnoxious weed of lawns and pastures. It is believed to have been imported into Central America as a contaminant in grass seed.

2. POLYGONUM L.

Polygonum L. Sp. Pl. 359. 1753.

Flowers perfect, occasionally with tendencies toward suppression of one sex, with pedicels distally articulated, usually in ochreolate fascicles. Perianth of 4–5

subequal partially connate tepals, white, green, red or pink. Stamens 5–8 (–9), the filaments discrete, often unequal in length, occasionally adnate to the tepals, the anthers small, versatile, introrse, often isodiametric and appearing peltate. Ovary lenticular or trigonous; styles 2 or 3, terminated by capitate stigmata. Achene usually included, lenticular or trigonous, often beaked, the facies ovate or orbicular. Annual or perennial herbs, sometimes clambering or twining, occasionally shrubby. Leaves alternate, mostly linear to ovate, occasionally sagittate, cordate or hastate, the blades mostly exceeding the petioles; ochreae usually conspicuous, often fringed with strigose cilia. Inflorescences of terminal spicate panicles, racemes or cymes, in some species the flowers solitary or fasciculate in the axils; rhachises glabrous to sericeous, occasionally glandular.

This largely temperate genus contains about 150 species, about half of which occur in North America. Many of the herbaceous species are aquatic or bog plants; some are rather obnoxious weeds. Shrubby species are often cultivated as ornamentals. The sections of the genus have often been elevated to generic status, but they are here maintained at the subgeneric level. Heterostyly, tendencies toward the suppression of one sex in the flowers, environmental modifications, and hybridization have all contributed to the difficult taxonomy of the section PERSICARIA, to which belong five of the six Panama species. Fourteen species are known from Guatemala and four from Costa Rica.

a. Plants not twining; leaf bases acute; inflorescences of terminal subspicate racemes or panicles; achenes lenticular or triquetrous; styles 2–3, partially discrete .... § PERSICARIA.
  b. Ochreae with reflexed or spreading herbaceous flanges; leaves mostly over 4 cm. wide; achenes lenticular .... 1. P. HISPIDUM
  bb. Ochreae unflanged, but often strigose-ciliate at the summit; leaves mostly less than 4 cm. wide; achenes lenticular or triquetrous ....
    c. Achenes triquetrous; styles 3; spikes filiform, lax, interrupted, with only the uppermost ochreolae imbricate.
      d. Tepals, leaves and ochreae conspicuously dark-punctate; midribs of the leaves subglabrous .... 2. P. PUNCTATUM
      dd. Tepals, leaves and ochreae inconspicuously pellucid-punctate; midribs of the leaves strigose or strigillose .... 3. P. HYDROPIPEROIDES
    cc. Achenes lenticular; styles 2; spikes cylindric, rigid, continuous, with all but the lowermost ochreolae imbricate.
      e. Facies of the achenes ovate; ochreae 2–3 cm. long, with apical strigose cilia to 1.5 cm. long; peduncles glandless; calyx white; leaves often conspicuously pubescent .... 4. P. ACUMINATUM
      ee. Facies of the achenes orbicular; ochreae 0.5–1.5 cm. long, eciliate at the summit; peduncles glandular; calyx pink; leaves, except for the veins, glabrous .... 5. P. MEXICANUM
aa. Plants twining; leaf bases cordate; inflorescences of lax axillary, frequently leafy, racemes or panicles; achenes triquetrous. Styles 3, united and capped by a 3-lobed capitate stigma .... § TINARIA. 6. P. CONVOLVULUS

1. POLYGONUM HISPIDUM HBK. Nov. Gen. & Sp. 2:178. 1817.

Robust glutinous-hispid perennials. Leaves punctate, hispid especially on the veins, entire but ciliate on the margins, apically attenuate, the bases decurrent on the petioles; blades broadly lanceolate to ovate, 10–30 cm. long, 5–9 cm. broad; ochreae 1–3.5 cm. long, hispid, the summits capped by herbaceous recurving flanges. Inflorescences of terminal continuous ochreolate subspicate racemes or

panicles, the peduncles strigose, the floriferous portions mostly 3–10 cm. long and 0.5–1 cm. broad, the flowers fascicled in ochreolae 2–4 mm. long. Flowers white to dark rose, the pedicels apically articulated and about equaling the ochreolae, 3–4 mm. long; tepals 5, subequal, the outer 4–5 mm. long, the inner somewhat shorter; stamens 5, discrete, affixed just above the base of the tepals; filaments 1.5–2 mm. long, the anthers about 0.5 mm. in diameter, subrotund, versatile, thus appearing peltate; ovary lenticular; styles 2, about 2 mm. long, connate for about 1 mm., the stigmata at anthesis about equaling the anthers. Achenes lenticular, orbicular, often with a concavity on one or both facies, black, lustrous, 3–4 mm. long, the persistent styles slightly over 1 mm. long.

CANAL ZONE: vicinity of Gatuncillo, *Piper 5624*. PANAMÁ: in swamps on edge of jungle; along road between Panamá and Chepo, *Dodge, Hunter, Steyermark & Allen 16672*.

This paludal or aquatic species, occurring chiefly at low elevations, is probably indigenous to South and Central America and the West Indies.

2. POLYGONUM PUNCTATUM Ell. Bot. S. C. & Ga. 1:445. 1817.

Polygonum hydropiper Michx. Fl. Bor. Am. 1:238. 1803. not L. 1753.
Polygonum hydropiperoides Pursh, Fl. Am. Sept. 270. 1814. not Michx. 1803.
Polygonum acre HBK. Nov. Gen. & Sp. 2:179. 1817.
Polygonum maritimum Vell. Fl. Flum. 4. *t. 39*. 1827.
Polygonum antihaemorrhoidale f. *riparium* Mart. Reise. 550. 1828.
Polygonum antihaemorrhoidale f. *aquatile* Mart. Reise. 550. 1828.
Polygonum antihaemorrhoidale α *riparium* Mart. in Linnaea 5: litt. 41. 1830.
Polygonum antihaemorrhoidale β *aquatile* Mart. loc. cit. 1830.
Polygonum acre α *aquatile* Meissn. in Mart. Fl. Bras. 5^1:18. 1855.
Polygonum acre β *riparium* Meissn. loc. cit. 18. 1855.
Polygonum acre α *confertiflorum* Meissn. in DC. Prodr. 14:108. 1856.
Polygonum acre β *leptostachyum* Meissn. loc. cit. 108. 1856.
Polygonum acre γ *brachystachyum* Meissn. loc. cit. 108. 1856.
Polygonum acre δ *majus* Meissn. loc. cit. 108. 1856.
Polygonum acre ε *riparium* Meissn. loc. cit. 108. 1856.
Polygonum punctatum eciliatum Small, in Bull. Torr. Club 20:214. 1893.
Polygonum punctatum robustior Small, in Bull. Torr. Club 21:477. 1894.
Persicaria punctata eciliata Small, Fl. SE. U. S. 379. 1903.
Persicaria punctata robustior Small, loc. cit. 379. 1903.
Persicaria robustior Bickn. in Bull. Torr. Club 36:455. 1909.
Persicaria punctata var. *tacubayana* Nieuwl. in Am. Midl. Nat. 3:131. 1913.
Polygonum robustius Fernald, in Rhodora 25:147. 1921.
Polygonum punctatum var. *parvum* Vict. & Rousseau, in Contr. Inst. Bot. Univ. Montr. 36:13. 1940.
Polygonum punctatum var. *aquatile* (Mart.) Fassett, in Caldasia 4:221. 1946.
Polygonum punctatum var. *aquatile* f. *stipitatum* Fassett, loc. cit. 223. 1946.
Polygonum punctatum var. *typicum* Fassett, in Brittonia 6:371. 1949.
Polygonum punctatum var. *tacubayanum* (Nieuwl.) Fassett, loc. cit. 374. 1949.
Polygonum punctatum var. *majus* (Meissn.) Fassett, loc. cit. 372. 1949.
Polygonum punctatum var. *ellipticum* Fassett, loc. cit. 375. 1949.
Polygonum punctatum var. *confertiflorum* (Meissn.) Fassett, loc. cit. 377. 1949.
Polygonum punctatum var. *confertiflorum* f. *longicollum* Fassett, loc. cit. 379. 1949.
Polygonum punctatum var. *littorale* Fassett, loc. cit. 379. 1949.
Polygonum punctatum var. *parviflorum* Fassett, loc. cit. 381. 1949.
Polygonum punctatum var. *mexicanum* Fassett, loc. cit. 381. 1949.
Polygonum punctatum var. *riparium* (Meissn.) Fassett, loc. cit. 382. 1949.

Fig. 104. A. Habit and details of *Polygonum punctatum*; seeds: B. *P. hydropiperoides*; C. *P. acuminatum*; D. *P. hispidum*; E. *P. mexicanum*; F. *P. convolvulus*.

Slender glabrous annuals or perennials, sometimes creeping and forming colonies. Leaves punctate with dark glands, subglabrous, entire but minutely ciliate on the margins, apically attenuate, the bases decurrent on the petioles; blades

lanceolate to narrowly ovate, 2–10 cm. long, 0.5–2 cm. broad; ochreae 0.5–1.5 cm. long, strigose-ciliate only apically. Inflorescences of terminal interrupted, often drooping, spicate racemes or panicles, the peduncles glabrous, the floriferous portions 5–15 cm. long, about 0.5 cm. broad, the flowers fascicled in ciliate ochreolae 2–3 mm. long. Flowers mostly white to greenish, the pedicels apically articulated and exceeding the ochreolae by 1–2 mm.; tepals 5, subequal, the outer 3–4 mm. long, the inner somewhat shorter, strongly punctate, ovate; stamens typically 8, discrete, affixed just above the base of the tepals; filaments 1–1.5 mm. long, the anthers less than 0.5 mm. in diameter, subrotund, versatile, thus appearing peltate; ovary trigonous; styles 3, about 1 mm. long, connate for about 0.5 mm.; stigmata capitate. Achenes triquetrous (in Panama), with ovate facies and inconspicuous beaks, brown to black, 2.5–4 mm. long.

CANAL ZONE: Gamboa, *Bro. Heriberto 37*; shore, end of Barro Colorado Island, *Bangham 571*; Joan Mina, *Piper 5694*; in water, Darién Station, *Standley 31578*. CHIRIQUÍ: vicinity of El Valle de Antón, ca. 600 m., *Allen 1986*; valle of the Upper Río Chiriquí Viejo, *P. White 38*; vicinity of Boquete, ca. 1300–1700 m., *Woodson, Allen & Seibert 1165*. COCLÉ: lower portion of valley and marshes along R. Antón, El Valle de Antón, ca. 500 m., *Hunter & Allen 354*; Penonomé and vicinity, 50–1000 ft., along stream, *Williams 60*; El Valle, valley floor and lower slopes along highway, *Miller 1834*. COLÓN: Ahorca Lagarto to Culebra, *Cowell 391*. PANAMÁ: Chepo, 100 ft., *Bro. Maurice 763*. PROVINCE UNKNOWN: western Panamá, *Stark 44*; *Sutton Hayes 968*.

This, the most commonly collected and perhaps most abundant species in Panama, ranges from southern Canada to Argentina. Some local Central American names are *chilillo, chilillo de perro* and *canilla de pava*. Decoctions of the acrid leaves are reported to be used in treating dogs suffering from mange. Those interested in infraspecific delineations are referred to the monograph of Fassett (in Rhodora 6:369. 1949.), in which twelve varieties, four to be expected in Panama, are treated. Fassett cites Panama specimens of vars. *aquatile* and *ellipticum*; vars. *confertiflorum* and *majus*, judging from their distributions, are to be expected in Panama. Closely allied *P. portoricense* Bert., with eciliate ochreae and ochreolae, is widespread in tropical America and might be expected in Panama.

3. POLYGONUM HYDROPIPEROIDES Michx. Fl. Bor. 1:239. 1803.

Polygonum barbatum Walt. Fl. Car. 131. 1788. not L.
Polygonum mite Persoon, Syn. Pl. 1:440. 1805.
Polygonum virgatum Cham. & Schlect. in Linnaea 3:45. 1828.
Polygonum hydropiperoides β virgatum Meissn. in Mart. Fl. Bras. 5^1:17. 1855.
Polygonum hydropiperoides var. *strigosum* Small, in Bull. Torr. Club 9:355. 1892.
Polygonum hydropiperoides macouni Small, in Mem. Dept. Bot. Col. Coll. 1:81. 1895.
Persicaria hydropiperoides (Michx.) Small, Fl. SE. U. S. 378. 1903.
Polygonum hydropiperoides f. *leucochranthum* Moore, in Rhodora 16:129. 1914.
Polygonum hydropiperoides var. *digitatum* Fernald, in Rhodora 23:260. 1922.
Polygonum hydropiperoides f. *strigosum* (Small) Stanford, in Rhodora 28:26. 1926.
Polygonum hydropiperoides var. *macerum* Stanford, loc. cit. 26. 1926.
Polygonum hydropiperoides var. *sanebelense* Stanford, loc. cit. 27. 1926.
Polygonum hydropiperoides var. *bushianum* Stanford, loc. cit. 27. 1926.
Polygonum hydropiperoides var. *asperifolium* Stanford, loc. cit. 27. 1926.

Slender subglabrous perennials, occasionally creeping and rooting at the lower

nodes. Leaves punctate with inconspicuous pellucid glands, usually strigillose on the veins below, entire but minutely ciliate on the margins, apically long-attenuate, the bases decurrent on the petioles; blades narrowly lanceolate, slightly falcate, 4–15 cm. long, 0.5–1.5 cm. broad; ochreae 1–3 cm. long, with apical cilia up to 8 mm. long. Inflorescences of terminal, lax, often drooping, subspicate racemes or panicles, the peduncles glabrous; floriferous portions interrupted, 5–15 cm. long, about 0.5 cm. broad, the flowers fasciculate in ciliate ochreolae 2–3 mm. long. Flowers mauve to greenish, the pedicels apically articulated and ultimately exceeding the ochreolae by about 1 mm.; tepals usually 5, subequal, ovate, becoming 2–3 mm. long; stamens usually 8, discrete, affixed just above the base of the tepals; filaments about 1 mm. long; anthers less than 0.5 mm. in diameter, subrotund, versatile, thus appearing peltate; ovary trigonous; styles 3, about 1 mm. long, connate for about 0.5 mm.; stigmata capitate. Achenes triquetrous (in Panama), with ovate facies and inconspicuous beaks, brown to black, 2–3 mm. long.

CANAL ZONE: Gigante Bay, Barro Colorado Island, *Shattuck 840*; Barro Colorado Island, *Kenoyer 347*.

Usually inhabiting meadows and stream banks, this species ranges from Canada to Central and South America, where it is supposed to merge with *P. persicarioides* HBK. In regions of Guatemala it is called *flor de chajutal* (fide Standley & Steyermark, in Field Mus. Bot. 24^4:126. 1946.). Intergradation, south of the continental borders of the United States, prompted Stanford (in Rhodora 28:25. 1926.) to reduce *P. persicarioides* HBK. to varietal status under *P. hydropiperoides.* In the Central American material however, *P. persicarioides* seems more distinct from *P. hydropiperoides* than does *P. punctatum.* Recent workers have probably rightly upheld *P. persicarioides* as a distinct species. It occurs at moderate elevations in Guatemala, Costa Rica and South America and is perhaps to be expected in Panama.

4. POLYGONUM ACUMINATUM HBK. Nov. Gen. & Sp. 2:178. 1817.

Polygonum cuspidatum Willd. in Spreng. Syst. 2:256. 1825.
Polygonum erectum Vell. Fl. Flum. 4: *t. 42.* 1827.
Polygonum setigerum Wedd. in Ann. Sci. Nat. 3^{13}:253. 1849.
Polygonum floribundum Wedd. loc. cit. 253. 1849.
Polygonum acuminatum α humboldtii Meissn. in DC. Prodr. 14:114. 1856.
Polygonum acuminatum β glabrescens Meissn. loc. cit. 114. 1856.
Polygonum acuminatum γ subcordatum Meissn. loc. cit. 114. 1856.
Polygonum acuminatum δ setigerum Meissn. loc. cit. 114. 1856.
Polygonum acuminatum ε brachystemon Meissn. loc. cit. 114. 1856.
Polygonum acuminatum ζ microstemon Meissn. loc. cit. 114. 1856.
Polygonum acuminatum η weddellii Meissn. loc. cit. 114. 1856.
Polygonum acuminatum θ capense Meissn. loc. cit. 114. 1856.
Persicaria acuminata (HBK.) Maza, in Per. Cub. 278. 1896.
Polygonum guatemalense Gandoger, in Bull. Bot. Soc. France 66:225. 1919.

Rather robust perennials, often conspicuously strigose or cinereous. Leaves punctate with inconspicuous pellucid glands, usually strigose or cinereous, strigose on the margins, apically long-attenuate, the bases abruptly decurrent on the

petioles; blades sessile or subsessile, lanceolate, falcate, 10–30 cm. long, 2–3.5 cm. broad; ochreae 2–3 cm. long, with apical strigose cilia up to 1.5 cm. long, strigose on the veins. Inflorescences of terminal rather rigid subspicate racemes or panicles, the peduncles strigose; floriferous portions continuous, 3–13 cm. long, almost 1 cm. broad, the flowers fasciculate in ciliate imbricate ochreolae 2–3.5 mm. long. Flowers whitish, the pedicels apically articulated and ultimately exceeding the ochreolae by 1–2 mm.; tepals 4 (–5), subequal, ovate, becoming 2.5–3.5 mm. long; stamens commonly 6, discrete, affixed just above the base of the tepals; filaments to 3 mm. long, with versatile anthers about 0.5 mm. long; ovary lenticular; styles 2, 2–3 mm. long, connate for about 0.5 mm.; stigmata capitate. Achenes lenticular, with ovate facies and a clearly delineated beak about 0.5 mm. long, brown to black, lustrous, 2–2.5 mm. long, 1.5–2 mm. broad.

CANAL ZONE: vicinity of Miraflores Lock, G. *White 187*; south end of island, P. *White 142*; Río Chagres, *Fairchild 2095*; vicinity of Gamboa, *Allen 1969*; Mindi, *Cowell 168*.

Inhabiting marshes and streams of low elevations, this species ranges from Mexico through Central America and South America to Argentina. In Guatemala it is called *chilillo* and *chilillo de clucho*. The typical varieties of *P. punctatum* and *P. hydropiperoides*, essentially North American varieties, grade into atypical varieties in the Caribbean countries, and here tend to approach the more southern speciees, *P. acuminatum* and *P. persicarioides*. This gradation is responsible for a serial relationship between these four species. Data suggesting this seriation are included in the following chart:

P. punctatum var. *punctatum*	*P. hydropiperoides* var. *hydropiperoides*	*P. persicarioides*	*P. acuminatum*
with dark punctation	with pellucid punctation	with pellucid punctation	with pellucid punctation
achenes strictly triquetrous	achenes strictly triquetrous	achenes lenticular and triquetrous	achenes strictly lenticular
spikes filiform and interrupted	spikes filiform and interrupted	spikes cylindric and continuous	spikes cylindric and continuous
leaves subglabrous	leaves subglabrous to strigillose below	leaves strigillose below	leaves strigose to sericeous

5. POLYGONUM MEXICANUM Small, in Bull. Torr. Bot. Club 19:256. 1892.

Polygonum pennsylvanicum Torr. Bot. Mex. Bound. Surv. 178. 1859. not L. 1753.
Persicaria mexicana Small, Fl. SE. U. S. 377. 1903.

Rather robust annuals, glabrous below, upwardly becoming glandular-hairy, sometimes decumbent and rooting at the lowermost nodes. Leaves conspicuously punctate, essentially glabrous except for the strigillose margins, apically long-attenuate, the bases gradually decurrent on petioles up to 1 cm. long; blades linear to lanceolate, falcate, 6–15 cm. long, 0.5–2.0 cm. broad; ochreae 0.5–1.5 cm. long, eciliate, glabrous. Inflorescences of terminal subspicate racemes or panicles, the peduncles glandular and strigose; floriferous portions continuous, 1–6 cm. long,

5–8 mm. broad, the flowers fasciculate in eciliate imbricate ochreolae 2–3 mm. long. Flowers pink, the pedicels distally articulated and mostly included in the ochreolae; tepals 4–5, subequal, ovate, becoming 2–3 mm. long; stamens 6–8, discrete, difficultly separable from the tepals; filaments filiform or flattened, 1–2.5 mm. long; anthers less than 0.5 mm. in diameter, subrotund, versatile, thus appearing peltate; ovary lenticular; styles 2, about 2 mm. long, connate for about 1 mm.; stigmata capitate. Achenes lenticular, orbiculate, the beak not prominent, brown to black, dull, 2–3 mm. long, 2–3 mm. broad.

PROVINCE UNKNOWN: Panamá, *Sutton Hayes 970*.

This aquatic or paludal species has a spotty distribution in Mexico and Central America and possibly in the southern United States. Colloquial names in Guatemala are *lechuga de agua* and *chilillo*. Small, in describing this species, emphasized its relationship to *P. pennsylvanicum* L. and did not compare it with *P. segetum* HBK., another very closely related species. Recent authors in their keys separate *P. segetum* from *P. mexicanum* by the former's ciliate ochreae, but this is an inconstant character; both were originally described as having eciliate ochreae. From the descriptions of Small (Fl. SE. U. S. 337. 1903.) and Stanford (in Rhodora 27:186. 1925.) it is concluded that the Panama specimen is *P. mexicanum* because of the orbicular achenes with short acute beaks, the achenes of *P. segetum* being ovoid with attenuate spinose beaks. These two species are separated by weak characters indeed and a concentrated study might demonstrate that they are conspecific.

6. POLYGONUM CONVOLVULUS L. Sp. Pl. 364. 1753.

Clambering or twining glabrous or scurfy annuals. Leaves inconspicuously punctate, often scurfy on the veins below, entire but strigillose on the margins, apically acute or attenuate, the bases not decurrent on the petioles; blades cordate, 1–6 cm. long, 0.5–5 cm. broad; ochreae 2–4 mm. long, fragile, usually eciliate. Inflorescences of axillary lax leafy racemes or panicles, the peduncles and rhachises scurfy, the flowers loosely fasciculate in mostly eciliate ochreolae 1–2 mm. long. Flowers greenish, the pedicels distally articulated and ultimately exceeding the ochreolae by 1–2 mm.; tepals 5, subequal, connate for about half their length, 3–4 mm. long; stamens 8, discrete, adnate for half their length to the tepals; filaments about 1.5 mm. long; anthers less than 0.5 mm. in diameter, subrotund; ovary trigonous; styles 3, connate, capped by a 3-lobate stigma, about 0.5 mm. long. Achenes triquetrous, with ovate facies, scarcely beaked, dull, black, granular, 3–4 mm. long.

CHIRIQUÍ: Cerro Punta, ca. 6025 ft., *P. White 198*.

This weedy species, naturalized from Europe, is quite common in temperate North America, but seems to be rather rare in Central and South America. The cited specimen is the only *P. convolvulus* from Central and South America in the herbarium of the Missouri Botanical Garden.

The section ECHINOCAULON Small is represented in Central America by *P. meissnerianum* Cham. & Schlecht., which differs from all the aforementioned in having clambering armed stems and glandular dichotomous few-flowered cymes and triquetrous achenes. In the Caribbean region it is found in Mexico, Guatemala, Salvador, Costa Rica and the West Indies but has not yet been collected in Panama. It ranges from the southeastern United States to Brazil. *Joinsson 167* from Paraná in Brazil, labeled as *P. meissnerianum,* is *P. arifolium* L., probably not previously reported from Brazil or even from South America.

3. ANTIGONON Endl.

ANTIGONON Endl. Gen. Pl. 310. 1836–40.

Corculum (Endl.) Stuntz, in U. S. D. A., Bur. Pl. Ind., Bull. 282:86. 1913.

Flowers perfect, with articulated pedicels, in ochreolate fascicles of 1–many. Perianth of 5 discrete unequal tepals, the outer 3 broader than the inner 2; tepals red or greenish white, slightly accrescent in fruit. Stamens 8, 2–3 mm. long, at first exceeding the stigmata; filaments united below into an occasionally appendiculate tube essentially free from the tepals; anthers 4-locular, introrse, versatile, about 0.5 mm. long. Ovary trigonous; styles 3, arcuate, terminated by peltate stigmata. Achenes mostly concealed by the tepals, bluntly 3-angled, usually brown and slightly lustrous. Capreolate vines scandent by tendrils terminating the inflorescences, the stems sulcate, herbaceous or suffrutescent, pubescent or glabrate. Leaves alternate, cordate to deltoid, acute to acuminate apically, the blades exceeding the alate or terete petioles; ochreae obsolete. Inflorescences of axillary and terminal racemes or panicles, the rhachises usually pubescent and terminated by tendrils.

This genus, indigenous to Mexico and Central America and cultivated elsewhere because of its handsome flowers and reputedly edible tubers, is here considered to consist of only three species. Due to the rapid migrations of cultivants, all three species are treated here, although *A. leptopus* is the only species so far collected in Panama. Stuntz (in U. S. D. A., Bur. Pl. Ind., Bull. 282:86. 1913.), in his widely overlooked paper, points out the similarity of the name *Antigonon* with *Antigona,* now reduced to synonomy with *Casearia* in the Flacourtiaceae. He concluded that *Antigonon* was homonymous with *Antigona* and proposed the generic name *Corculum.* International rules of nomenclature allow the existence of *Peponia* and *Peponium* so apparently different singular genders are not regarded as homonyms or orthographic variants. Consequently the generic name *Antigonon* should be maintained.

a. Outer tepals at anthesis longer than broad, cordate, minutely pubescent without, rarely stipitate-glandular within; petioles alate or terete, pubescent or glabrous, longer than the sinus of the cordate to truncate leaf base, mostly more than 1 cm. long.
  b. Tepals reddish, in fruit less than 1.5 times as long as broad; achene included; petioles terete or alate........ 1. A. LEPTOPUS
  bb. Tepals greenish white, in fruit mostly more than 1.5 times as long as broad; achene slightly exserted; petioles alate........ 2. A. FLAVESCENS
aa. Outer tepals at anthesis at least as broad as long, rounded at both ends, closely tomentose without, stipitate-glandular within; petioles mostly terete, shorter than the sinus of the cordate leaf base, mostly less than 1 cm. long........ 3. A. GUATEMALENSE

1. ANTIGONON LEPTOPUS Hook. & Arn. Bot. Beech. Voy. 308. 1840.

Antigonon platypus Hook. & Arn. loc. cit. 309. 1840.
Antigonon cordatum Mart. & Gal. in Bull. Acad. Brux. 10^1:354. 1843.
Antigonon cinerascens Mart. & Gal. loc. cit. 355. 1843.
Corculum leptopus (Hook. & Arn.) Stuntz, in U. S. D. A., Bur. Pl. Ind., Bull. 282:86. 1913.

Glabrous to densely cinereous- or rufous-pubescent tuberous vines. Leaves broadly cordate to narrowly deltoid, acute to acuminate, often mucronate; blades mostly 3–14 cm. long, 2–12 cm. broad, glabrate to closely pubescent below; petioles mostly 1–2.5 cm. long, glabrous to pubescent, the leaf bases occasionally decurrent

Fig. 105. *Antigonon leptopus*

on the petioles forming flanges up to 5 mm. wide. Inflorescences of axillary and terminal capreolate racemes or panicles, the rhachises glabrate to densely pubescent. Flowers pedicellate, the glabrous to densely pubescent pedicels mostly articulated below the middle; tepals pink to purplish, cordate, in fruit 8–25 mm. long, 4–20 mm. broad, glabrous to closely pubescent without, rarely stipitate-glandular within; stamens 8, connate about half their length to form a filament tube, often with 1 tooth intercalated between the free portions of adjacent filaments; ovary trigonous; styles 3, arcuate; stigmata peltate. Achenes bluntly triquetrous, usually included, about 1 cm. long.

CANAL ZONE: Balboa, *Standley 25533*; Balboa, *Standley 28551*; Chiva-chiva trail 2 mi. above Red Tank, *Maxon & Harvey 6612*; Matachín to Las Cascadas, *Cowell 357*. PANAMÁ: O. U. Experiment Station, 3 mi. e. of Panamá City, *Maxon, Harvey & Valentine 7088*.

This species is widely cultivated and escaped and determination of its natural range would be difficult. It is cultivated in Florida where it is called "confederate vine". In the West Indies it is called *corallina* and *corallillo*. In Mexico, where it is supposed to have originated, it is called *coronilla* and *chaclomacal*. Other Central American names are *confite, flor de san miguel, san diego, bellísima, colación* and *confite rojo*. In the Canal Zone it is called "coralvine", *coralito, enredadera* and *cadena de amor*. In Panamá and the Canal Zone, *A. leptopus* seems to be fairly well established. A variant commonly called *A. cinerascens*,* which seems to differ regularly only in its dilated petioles, might also be cultivated here. Comparison of specimens with and without the dilated petioles has revealed no correlated differences. Hence it is concluded that *A. platypus* (*A. cinerascens*) is conspecific with *A. leptopus*.

2. ANTIGONON FLAVESCENS Watson, in Proc. Am. Acad. 22:446. 1887.

Finely pubescent tuberous vines. Leaves narrowly cordate to deltoid, acute, mucronate, the blades mostly about 8 cm. long by 6 cm. broad, pubescent on the veins below; petioles 1–2 cm. long, sparsely pubescent, the leaf bases decurrent on the petioles forming flanges up to 4 mm. broad. Inflorescences of axillary and terminal capreolate racemes or panicles, the rhachises rufous-pubescent. Flowers pedicellate, the minutely pubescent pedicels articulated 2–3 mm. from the rhachis, 7–10 mm. long; tepals greenish white, cordate, acute, in fruit about 10 mm. long by 4 mm. broad, glabrate; stamens 8, connate slightly less than half their length, about 2 mm. long; ovary trigonous; styles 3, arcuate; stigmata peltate. Achenes bluntly triquetrous, about 11 mm. long, slightly exserted.

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* The epithet *cinerascens* Mart. & Gal. is antedated three years by the epithet *platypus* Hook. & Arn., published in a footnote. The type of *A. platypus* is *Andrieux 117* and a paratype is *Andrieux 116*. Meissner (in DC. Prodr. 14:184. 1856.) applied the name *A. cordatum* Mart. & Gal. to the type and *A. cinerascens* to the paratype, apparently using the epithets and scarcely diagnostic descriptions of Martens & Galeotti and overlooking the epithet *platypus*. Thus plants with dilated petioles have been passing as *A. cinerascens* rather than *A. platypus*, the earlier name. Recent workers have attributed darker tepals to *A. cinerascens* than to *A. leptopus* but Martens & Galeotti make no such distinction but compare them as "également rose". I feel, just as Hooker & Arnott suggested (Bot. Beech. Voy. 309. 1840.), that there is only one species involved.

This lochmophilous species is known only from Mexico and Guatemala. Due to the inferior color of its tepals, it is less likely to be cultivated than other species. In characters other than color this species is very similar to some of the narrow-tepaled forms of *A. leptopus.* Although the flowers of a specimen labeled *A. flavescens, Pringle 4570,* collected in Jalisco, are annotated by C. H. Thompson (Oct. 10, 1898) as "all right for *A. flavescens*", the fruiting tepals are broadly ovate. If this annotation is correct, there is little doubt that *A. flavescens* is but a color form of *A. leptopus.* Watson (in Proc. Am. Acad. 22:446. 1887.) offered no supporting character for color save the narrower tepals. I strongly suspect that *A. flavescens* is merely a color form of *A. leptopus.* On the contrary, Standley & Steyermark (in Field Mus. Bot. 24^4:106. 1946.) believe it to be a good species.

3. ANTIGONON GUATEMALENSE Meissn. in DC. Prodr. 14:184. 1856.

Polygonum grandiflorum Bertol. Fl. Guat. 412. 1840. not Willd. 1799.
Antigonon grandiflorum (Bertol.) Robinson, in Proc. Am. Acad. 44:613. 1909.
Antigonon macrocarpum Britton & Small, in Britton & Wilson, in N. Y. Acad Sci. 5^2:266. 1924:

Cinereous tuberous vines. Leaves broadly cordate, abruptly acuminate, mucronate, the blades 3–9 cm. long, 2.5–7 cm. broad, closely cinereous-pubescent below; petioles mostly less than 1 cm. long, cinereous-pubescent, terete, the leaf bases not decurrent. Inflorescences of axillary and terminal capreolate racemes or panicles, the rhachises cinereous-pubescent. Flowers pedicellate, the pedicels medially articulated, with a change in degree of pubescence at the point of articulation, becoming 10–15 mm. long; tepals pink, at anthesis as broad as long, about 1 cm. long, closely cinereous-pubescent without, stipitate-glandular within; stamens 8, connate about one fourth their length, about 2 mm. long; ovary trigonous; styles 3, arcuate; stigmata peltate. Mature achenes not seen.

This species, an inhabitant of thickets, is often cultivated. No specimens have been seen from Panama. It has been collected in Mexico, Guatemala, Salvador, Nicaragua, Costa Rica and the West Indies. Colloquial names reported to be applied in Salvador are *colación, confite* and *san andrés.*

4. MUEHLENBECKIA Meissn.

MUEHLENBECKIA Meissn. Gen. Pl. 2:227. 1840. nom. conserv.

Calacinum Raf. Fl. Tellur. 2:33. 1836.
Karkinetron Raf. Fl. Tellur. 5:11. 1836.
Sarcogonum G. Don. in Sweet, Hort. Brit. 3:577. 1839.
Conobaea Bert. in Steud. Nom. Bot. 2^1:404. 1840.

Flowers polygamo-subdioecious (perfect in some spp. outside Panama), with short pedicels articulated at the base of the tepals, 1–5 (–many) in fascicles subtended by telescoped ochreolae. Tepals 5 (6, 4), subequal, greenish white, slightly accrescent and becoming more or less fused with the achene basally. Stamens 8 (–10), 1–3 mm. long, inserted on the base of the tepals, discrete or forming an inconspicuous annular disc, reduced or absent in pistillate flowers; anthers 4-locular,

introrse, versatile. Ovary trigonous, reduced or absent in staminate flowers; styles 3, short, arcuate; stigmata capitate, lobate, or fimbrillate. Achenes mostly included, bluntly to acutely triquetrous, dark, lustrous, often puncticulate. Scramblers or low matted shrubs with usually glabrous, often sulcate stems. Leaves alternate, entire, apically acuminate to acute, basally hastate, cordate or acute, the blades usually exceeding the petioles; ochreae hyaline and conspicuous, deciduous. Inflorescences of axillary panicles, racemes or glomerules, occasionally leafy.

This genus of some twenty species occurs chiefly in tropical American and Australian areas, often in alpine regions. In Central America are two indigens, *M. tamnifolia* and *M. volcanica.* Only *M. tamnifolia* has been collected in Panama. *M. volcanica,* a low mat-forming alpine shrub with the flowers solitary or fasciculate in the axils of the small elliptic leaves, inhabits the high mountains of Guatemala and western South America from Bolivia to Ecuador. *M. platyclada,* with the stem conspicuously flattened, is often cultivated in the Americas as a bizarre ornamental. It is a native of the Solomon Islands.

1. Muehlenbeckia tamnifolia (HBK.) Meissn. Gen. Pl. 2:227. 1840.

Polygonum tamnifolium HBK. Nov. Gen. & Sp. 2:180. 1817.
Polygonum flexuosum Benth. Pl. Hartw. 80. 1839.
Polygonum quadrangulatum Mart. & Gal. in Bull. Acad. Brux. 10^1:353. 1843.
Muehlenbeckie Benthamii Endl. Gen. Suppl. 4:51. 1847.
Muehlenbeckia quadrangulata Endl. loc. cit. 51. 1847.
Muehlenbeckia tamnifolia α Humboldtii Meissn. in DC. Prodr. 14. 149. 1856.
Muehlenbeckia tamnifolia β quadrangulata Meissn. loc. cit. 149. 1856.
Muehlenbeckia tamnifolia γ Hartwegii Meissn. loc. cit. 149. 1856.
Muehlenbeckia tamnifolia δ laxiflora Meissn. loc. cit. 149. 1856.
Muehlenbeckia leptobotrys Meissn. loc. cit. 149. 1856.
Muehlenbeckia Stuebelii Lindau, in Hieron. in Bot. Jahrb. 21:307. 1895.
Sarcogonum tamnifolium Rusby, in Mem. Torr. Club 6:111. 1896.
Calacinum tamnifolium (HBK.) Macbr. in Field Mus. Bot. 4:116. 1927.
Calacinum leptobotrys (Meissn.) Macbr. loc. cit. 116. 1927.

Clambering glabrous lianas, the branches smooth and sulcate, often angulate. Leaves glabrous, ovate, apically usually abruptly acuminate, basally hastate or cordate to acute, the blades mostly 3–8 cm. long, 1.5–4 cm. broad; petioles mostly 8–20 mm. long, glabrous, terete or canaliculate. Inflorescences chiefly of axillary racemes or panicles, the rhachises glabrous, rarely with reduced leaves. Flowers short-pedicellate, the pedicels apically articulated, 0.5–3 mm. long; tepals mostly five, greenish white, ovate, apically subacute to rounded, slightly connate basally, 1.5–3 mm. long, 1–2 mm. broad, glabrous; staminate flowers with 8 (–10) mostly separate stamens about 1 mm. long attached to the lower half of the tepals, the anthers introrse and versatile, about 0.5 mm. long, the ovary a short 3-styled rudiment or absent; pistillate flowers with trigonous superior ovaries with ovate facies; styles 3, strongly arcuate; stigmata fimbrillate-flabellate; stamens reduced to subsessile staminodia. Achenes bluntly trigonous, usually included by the tepals and hardly separable from their bases, often capped by an amorphous mass of stylar

tissue, smooth or slightly verrucose, dark, lustrous, 2–3 mm. long, nearly or quite as broad.

CHIRIQUÍ: R. Chiriquí Viejo, near Monte Lirio, G. *White 65*; Bajo Chorro, Boquete Dist., *Davidson 177*; vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 921*; trail from Paso Ancho to Monte Lirio, *Allen 1507*; Bajo Mono-Robalo trail, western slope of Cerro Horqueta, *Allen 4812*. PROVINCE UNKNOWN: *Sutton Hayes 486, 983*.

Often forming tangles in thickets or forests, this species ranges from southern Mexico through Central America and western South America to Argentina. In Costa Rica it is called *bejuco colorado*. A decoction of the leaves was once considered anti-hemorrhagic (fide HBK. Nov. Gen. & Sp. 2:180. 1817.). It is perhaps just coincidental that most specimens from Costa Rica and Panama have rounded to acute leaf bases and in other respects match the description of *M. stuebelii* Lind., a Colombian variant differing chiefly by its attenuate leaf bases and smaller inflorescences exceeded by the leaves. *Allen 4812* with both acute and subcordate leaf bases clearly shows that the leaf base is of little taxonomic significance in *M. tamnifolia*. Since many specimens with acute leaf bases have inflorescences clearly exceeding the leaves, it is concluded that *M. stuebelii* is conspecific with *M. tamnifolia*.

Fig. 106. *Muehlenbeckia tamnifolia*

5. COCCOLOBA P. Br. ex L.

By RICHARD A. HOWARD

Coccoloba P. Br. ex L. Syst. Nat. ed. 10. 1007, 1367. 1759. Taxon 3:114, 156, 233. 1954, nom. conserv. Howard, Jour. Arnold Arb. 40:176–220. 1959.

Guaiabara Miller, Gard. Dict. ed. 4. 2. 1754.
Coccolobis P. Br. Civ. & Nat. Hist. Jam. 209. *pl. 14, f. 3.* 1756.

Shrubs or trees, trees with scrambling branches, or lianas; branches terete or stout, commonly strongly striate, short shoots commonly developed laterally, or the terminal shoots of limited growth becoming long shoots, pith solid or the stem hollow except at the nodes; nodes commonly swollen; ocreae characteristically developed, sheathing at first, becoming split along one or two sides, the basal portion commonly coriaceous and persistent, the apical portion commonly membranaceous and deciduous or entirely membranaceous and deciduous, glabrous, puberulent or silky pubescent; leaves alternate, persistent or deciduous, membranaceous, chartaceous or coriaceous, on deciduous trees the young leaves usually turning black on drying, varying considerably in size on the same shoots, the leaves of adventitious or juvenile shoots commonly much larger and frequently of different shape from those of normal shoots; the petiole borne at the base of, or well above the base of, the ocrea, petioles slender to stout, commonly canaliculate above, glabrous to puberulent or pubescent; leaf blades with margins flat to slightly recurved, straight or undulate, midrib commonly keeled above and often below, primary veins straight to the margin or branched near the margin becoming reticulate, or arcuate and anastomosing, or arcuate and bifurcate-anastomosing, the secondary venation parallel or reticulate, conspicuous to obscure, leaf surface glabrous, puberulent or pilose becoming glabrate, pubescence often mixed with glandular-like bodies which are either hair bases or resinous excretions from the stomata or rarely multicellular glands; inflorescence terminal or terminal on lateral shoots, paniculate, racemose or spicate, the peduncle usually short; basal ocrea present, flowers functionally unisexual, the staminate flowers borne in clusters of 2–7, the pistillate flowers usually borne singly at each nodule on the rachis, rachis swollen at each flower cluster or terete, flowering clusters distinct or confluent, subtended by a small bract and one or more membranaceous ocreolae, ocreolae usually covering the flower bud and splitting regularly or irregularly forming a membranaceous collar or sheath, or one, two or more appendages, pedicels short or well developed, equaling or exceeding the ocreolae, hypanthium well developed or slight, perianth lobes usually 5, rarely to 7 in number, imbricate in bud, often reflexed at maturity, stamens usually 8, functional stamens exserted, non-functional stamens included, filaments commonly flared at the base and more or less united, functional pistil exserted, the non-functional pistil included, ovary strongly trigonous, glabrous, functional styles 3, or if 2 or 1 the non-functional styles filamentous, stigmatic surface often expanded; hypanthium and perianth lobes expanding in fruit, or only the perianth lobes expanding to cover the achene, fruiting hypanthium when fresh commonly brightly colored and fleshy, usually

astringent to taste, occasionally strongly fibrous; the achene trigonous in outline, black, brown or tan in color, shiny or dull, the outer wall hard, the inner layer papery, seed with ruminate endosperm, the major lobes 3, the minor lobes and involutions numerous, the embryo centrally located, the cotyledons orbicular, flat, rarely folded or contorted, the radicle small and terete.

Type: *Coccoloba uvifera* (L.) L. (*Polygonum uvifera* L.), probably from Jamaica.

a. Petioles arising from well above the base of ocrea, the diameter of the leaf-scar smaller than the distance to the base of the ocrea.
b. Inflorescence paniculate.
c. Inflorescence few branched; leaf base rounded or cordate; fruit spherical, rounded at the base .... 1. C. LASSERI
cc. Inflorescence many branched; leaf blade acute at the base, decurrent on the petiole; fruit oval, stalked at the base .... 2. C. TUERCKHEIMII
bb. Inflorescence racemose or spicate.
d. Inflorescence racemose; the fruits clearly stalked .... 3. C. CORONATA
dd. Inflorescence spicate; the fruits essentially sessile .... 4. C. OBOVATA
aa. Petioles arising from the base of the ocrea, the diameter of the leaf-scar greater than the distance from the base of the ocrea.
f. Inflorescence racemose.
g. Lianas; leaves usually oblong-elliptic and bullate between the veins. 5. C. PARIMENSIS
gg. Trees or shrubs; the branches not climbing.
h. Leaves as broad as or broader than long, orbicular to broadly oblong, apex rounded to emarginate; fruit obpyriform, obtuse and rounded at the apex, the perianth lobes imbricate .... 6. C. UVIFERA
hh. Leaves longer than broad.
i. Foliar ocrea 3–5 cm. long, membranaceous or chartaceous, silky pubescent; fruit coronate at the apex, the crown surrounded by the distinct perianth lobes .... 7. C. MANZANILLENSIS
ii. Foliar ocrea 1–2 cm. long, coriaceous or if chartaceous not silky pubescent; fruit not coronate, the perianth lobes imbricate, covering at least the upper half of the achene.
j. Inflorescence strongly sulcate or striate, the flower clusters closely associated and not appearing interrupted, rachis and bracts, ocreolae and perianth densely puberulent; mature fruit with perianth lobes distinct to the base .... 8. C. DARIENENSIS
jj. Inflorescence terete, not noticeably sulcate or striate, the flower clusters clearly distinct and separate on the axis, rachis and flowers scarcely puberulent or glabrous.
k. Leaves narrowly oblong, thick coriaceous, drying pale green or tan, the ultimate venation indistinct; fruit spherical, the perianth lobes surrounding the upper half of the achene .... 9. C. PADIFORMIS
kk. Leaves elliptic to elliptic-oblong, thin coriaceous, drying dark green or black, the ultimate venation clearly distinct and reticulate; fruit ovoid, the apex obtuse or acute, the perianth lobes distinct to the base, hypanthium scarcely evident .... 10. C. LEHMANNII
ff. Inflorescence spicate, the pedicels shorter than the ocreolae and the bracts in flower and fruit or if protruding beyond the ocreolae the visible portion less than the diameter of the inflorescence axis; perianth lobes expanding and covering at least the upper half of the mature achene.
l. Leaves lanceolate to ovate-lanceolate, the apex acuminate; inflorescence axis swollen at the flower clusters and tapering below each cluster .... 11. C. ACUMINATA
ll. Leaves oval to orbicular, the apex rounded or emarginate; the inflorescence axis of uniform thickness not expanded at each flower cluster .... 12. C. CARACASANA

1. COCCOLOBA LASSERI Lundell, Contr. Univ. Mich. Herb. 6:10. 1941.

Tree to 12 m. tall; branchlets thick, striate, puberulent; ocreae cylindrical and flaring at the top, to 1.5 cm. long, subtruncate, membranaceous above the petiole, densely puberulent when young, the petiole inserted at or above the middle; petioles minutely puberulent, stout, striate, 3–8 mm. long; blades obovate or oblanceolate-obovate, 12 × 5, 15 × 8, 19 × 10.5 cm. long and broad on fertile branches, chartaceous, glabrous above, puberulent below on the midrib and primary veins, apex rounded to obtusely-acute, attenuate from above the middle to the base, the base emarginate or rounded, primary veins 8–12 on each side; adventitious shoots and their leaves unknown; inflorescences terminating short lateral branches, rarely terminal, paniculate, the panicles sessile, composed of 3 or 4 racemes, the racemes to 30 cm. long, peduncles of racemes to 1.5 cm. long, the rachis densely puberulent, striate; staminate flowers borne in clusters of 3–6, pistillate flowers borne singly, bracts and ocreolae minute, less than 0.5 mm. long, the ocreolae multiple, membranaceous, pedicels 1–1.3 mm. long, puberulent, hypanthium about 1 mm. long, contracted into a short stipe, perianth lobes suborbicular, about 1 mm. in diameter, fertile stamens slightly exceeding the perianth lobes, functional pistil 2–3 mm. long, the styles 2 or 3, fruiting pedicels 1–1.3 mm. long, the mature fruit nearly spherical, the perianth lobes imbricate, about ⅓ the length of the fruit; the achene light brown, not coronate at the apex.

Common name: "uvero".

Collected in flower in May, June, September and November. Collected in fruit in August and December.

Recorded altitude, the tidal belt to 20 m.

COCLÉ: Aguadulce, *Pittier 4980*; Penonomé, *Williams 357*; *Stern, Chambers, Dwyer & Ebinger 989*. HERRERA: Chitré, *Allen 1111*; Mangle Dejunco, *Steyermark, Allen & Dodge s. n.* PANAMÁ: Bejuco, *Allen 2542*; Panamá Nat. Highway, Las Lajas Bridge, *Bartlett & Lasser 16638*; Río Pacora, *Bartlett & Lasser 16046* (Holotype, MICH.); Balboa to Chamé, *Dodge, Hunter, Steyermark & Allen 16732*; Punta Paitilla, *Standley 26265*. PROVINCE UNKNOWN: *Duchassaing s. n.* (collected 1851).

Here regarded as endemic to Panama. *Coccoloba lasseri* is very similar to *C. tuerckheimii*, differing in its smaller leaves, smaller inflorescence and nearly spherical fruits. A study of young plants, vigorous shoot growth or adventitious growth may well prove this species to be the same as *C. tuerckheimii.*

2. COCCOLOBA TUERCKHEIMII Donnell Smith, Bot. Gaz. 37:213. 1904.

Large tree to 15 m. tall; branches stout, striate, the internodes frequently shortened and compacted, forming areas of short shoot growth, lateral shoots, particularly flowering branches, distinct as short shoots; ocreae to 3 cm. long, large and conspicuous, coriaceous, strongly striate and persistent at the base, membranaceous and deciduous at the apex, puberulent becoming glabrate; petioles borne 6–15 mm. above the base of the ocreae, 1.5–3.5 cm. long, usually striate and slender, puberulent when young; blades oblong-ovate, abruptly short acuminate at the apex, the base acute and decurrent on the petiole, 13 × 7, 25 × 12 to 45 × 25 cm. long and wide, thinly coriaceous, glabrous above, puberulent below

Fig. 107. *Coccoloba lasseri*

when young, remaining so on the midrib and veins, primary veins 7–10 on each side, occasionally nearly barbate in the axils of the midrib and the veins on each side; inflorescence generally terminal on lateral short shoots, paniculate, the ocreae coriaceous, flaring, striate, 1 cm. long, the panicle almost sessile, peduncle short, 1–3 cm. long, racemes numerous, 10–19, each 10–35 cm. long, rachis and all parts puberulent, staminate flowers in clusters of 4–7, pistillate flowers borne singly at each nodule, bracts small, broadly triangular, less than 0.5 mm. long, ocreolae shorter than to scarcely exceeding the bracts, pedicels 2–3 mm. long, hypanthium conical 0.75 mm. long, perianth lobes oblong, 1–1.5 mm. long, 1 mm. wide, fertile stamens on filaments 3 mm. long, fertile pistil 3 mm. long; fruiting pedicels 2–3 mm. long, fruit oval, 11–14 mm. long, 6–9 mm. in diameter, the apex obtuse and slightly coronate, the perianth lobes surrounding the apex of the achene, the base of the fruit constricted to a stalk 1–2 mm. long; achene dark brown, obtusely trigonous in outline.

Type: *von Tuerckheim 8493*, Cubilqüitz, Dept. Alta Verapaz, Guatemala.

Collected in flower in August. Collected in fruit in July.

Guatemala, Honduras, Nicaragua, Costa Rica, Panama.

BOCAS DEL TORO: Changuinola valley, Island of Potrero, *Dunlap 181*. COLON: Dos Bocas, Río Fató valley, *Pittier 4197*.

3. COCCOLOBA CORONATA Jacquin, Enum. Pl. Carib. 19. 1760, Select, Stirp. Am. Hist. 114, *t. 77*. 1763; Dugand, Caldasia 4:427. 1947; Howard, Jour. Arnold Arb. 41:40, 226, 227. 1960.

Coccoloba novogranatensis Lindau, Engl. Bot. Jahrb. 13:192. 1890.
Coccoloba caribaea Urban, Symb. Ant. 5:377. 1907.
Coccoloba waitii Johnston, Sargentia 8:122. 1949.

Shrub, 3 m., or tree, 15m.; trunk commonly muscular, bark red; branchlets terete, glabrous, gray, the nodes slightly swollen; ocreae cylindrical, the upper portion membranaceous and deciduous, the lower portion coriaceous and persistent; leaves of normal shoots with petioles 8–11 mm. long, puberulent when young, with age glabrous except in the groove, attached above the base of the ocreae; blades ovate to oblong-ovate to ovate-elliptic, 6 × 4, 9 × 4, 10.5 × 5.5 cm. long and broad, thin-coriaceous, glabrous above, glabrate below except for long hairs along the midrib at the base of the blade, the apex attenuate, the base narrowly cordate, the margin entire, midrib and primary veins inconspicuous above, prominent below, the primary veins 5 or 6 pairs, the ultimate venation finely reticulate; leaves of adventitious shoots generally similar but occasionally obovate and narrowed at the base to ovate-lanceolate or lanceolate-elliptic, the blades 11 × 7 to 18 × 15 cm. long and broad, the basal lobes of leaves of adventitious shoots often overlapping; inflorescence terminal on short lateral shoots, 3–9 cm. long, the basal ocreae 5–10 mm. long, bilobed at the apex, the rachis glabrous, flowers commonly borne singly at each node, but occasionally two together in staminate plants, the bracts oblong, 2 mm. long, 0.5–0.75 mm. broad, the ocreolae 3 mm. long, bilobed at the apex, membranaceous and persistent, the pedicels 2.5–4 mm. long, the hypanthium 0.75 mm. long, the perianth lobes ovate, 1.5 mm. long and broad, the

functional stamens 2.5 mm. long, the functional pistil 2 mm. long; fruit generally spherical with coronate lobes, occasionally narrowed at the base, 1 cm. long, 5–9 mm. in diameter; the achene brown, shining.

Collected in flower in May. Collected in fruit in July, September and November.

St. Vincent, Grenada, Trinidad, Tobago, Margarita, Venezuela, Colombia, Peru, Guatemala, Panama.

DARIÉN: Cana, *Williams 945*. HERRERA: Pesé, *Allen 802*. PANAMÁ: Perlas Islands, Pedro Gonzalez, *Allen 2602*; San José Islands, *Erlanson 377, 550, 216*; *Harlow 41*; *Johnston 213, 230* (GH–type of *C. waitii*) *957, 1306*.

Although most of the specimens cited have been collected in coastal areas or at low elevations, the specimens by *R. S. Williams 945* were collected at 2800 ft. altitude. This collection is young material but appears to be safely referred here.

There appears to be no specimen preserved that was collected by Jacquin. However, the description and illustration are sufficiently specific and can serve as the nomenclatural type.

4. COCCOLOBA OBOVATA HBK. Nov. Gen. 2:176. 1817.

Coccoloba Goudotiana Wedd. Ann. Sci. Nat. III, 13:260. 1850.
Coccoloba riparia Lundell, Contr. Univ. Mich. Herb. 6:11. 1941.

Shrub of 3 m. to tree 15 m. tall; branches terete, glabrous; ocreae oblique, truncate, 7–10 mm. long, glabrous, membranaceous, striate, appressed; leaves of normal shoots with petioles 12–15 mm. long, pilose or glabrous, inserted above the base of the ocreae, blades obovate to subround-obovate, rarely ovate-lanceolate to elliptic obovate, 9 × 6, 10 × 4, 16 × 8 to 24 × 9.5 cm. long and wide, apex obtusely acuminate, base slightly cordate, coriaceous, turning dark brown or black on drying, tomentulose on the midrib and veins, persistent, short pilose in the axils of the veins and midrib, commonly densely covered with globose or peltate excretions associated with the stomata; leaves of adventitious shoots with petioles 3.5–6 cm. long, blades broadly elliptic-ovate to elliptic-oblong, 28 × 14 to 37 × 26 cm. long and wide; inflorescence terminal, solitary, densely flowered, staminate to 25 cm. long, pistillate to 17 cm. long, the flowers borne singly in the pistillate and in clusters of 4 in the staminate, peduncle, rachis, bracts and ocreolae short pilose, bracts semi-orbicular, 0.75 mm. long, ocreolae bilobed 1.5 mm. long, membranaceous, usually in multiples, pedicels included in the ocreolae in flower, exserted and to 1.5 mm. long in fruit, hypanthium 0.75 mm. long, the lobes ovate or nearly orbicular, to 1 mm. long, functional stamens exserted, sterile stamens included, ovary triangular, styles 3; fruit globose, obtusely-trigonous, strongly striate, the base rounded, the apex obtusely coronate, 6 mm. long, 5.5 mm. in diameter; achene tan to dark brown, trigonous.

Type: Colombia, prov. Tolima, Honda, *Humboldt s. n.* June 1805 (Herb. Willd. 7704), isotype Paris.

Common name: "Papaturra blanca", "Peña blanca".

Collected in flower in March, June, July, September and December. Collected in fruit in August and December.

Altitude range: 50 to 800 m.

Costa Rica, Panama, Colombia.

CANAL ZONE: Barro Colorado Island, *Aviles 998, Salvoza 984, Shattuck 1063, Starry 298*; F. L. Island, *Bangham 593*; Salamanca Hydrographic Station, *Dodge, Steyermark & Allen 16983, 16983a, Woodson, Allen & Seibert 1572*; northwestern part of Canal Zone, *Johnston 1519*; between Tumba Vieja and Salamanca, *Steyermark & Allen 16758*. CHIRIQUÍ: Cerro Galera Chorcha, Gualaca, *Allen 5020*; San Félix, *Allen 3655*; between San Félix and Cerro Flor, *Allen 1917*; Progreso, *Cooper & Slater 270*; San Bertolomé, *Woodson & Schery 947*; between Río Chiriquí and Remedios, *Woodson, Allen & Seibert 1182*. COCLÉ: El Valle, *Allen 2229* (MICH–holotype of *C. riparia*). VERAGUAS: between Santiago and David, *Stern, Chambers, Dwyer and Ebinger 999*.

5. COCCOLOBA PARIMENSIS Bentham, Hook. Lond. Jour. Bot. 4:626. 1845.

Coccoloba bracteolosa Lundell, Contr. Univ. Mich. Herb. 6:9. 1941, not Meisner.
Coccoloba leptostachya Standley, Contr. Arn. Arb. 5:62. 1933, not Bentham.

Tree to 8 m. with scrambling branches or a liana reaching 44 m.; stems slender, striate, minutely puberulent becoming glabrous, sparsely glandular; ocreae membranaceous, split and flaring at the apex, 2–2.5 cm. long, puberulent, usually decidous to the petiole; petioles arising from the base of the ocrea, slender, 1.5–2 cm. long on fertile shoots, puberulent; blades oblong-elliptic to elliptic-ovate, 8.5 × 4.5, 13.5 × 7 to 21 × 15 cm. long and broad, membranaceous when young becoming thin-coriaceous when mature, flat to noticeably bullate between the veins, puberulent to short pilose on the midrib and veins, puberulent to glabrate, usually sparsely glandular between the veins, apex short acuminate to obtuse, the base rounded, primary veins 6–9 on each side; leaves of sterile shoots larger, on petioles 5–6 cm. long, the blades to 27 × 16 cm. long and broad, the apex rounded and apiculate, the base truncate to cordate; inflorescence terminal on short lateral branches, usually solitary, all parts puberulent, staminate inflorescence 15 cm. long, the flowers 2–7 at each nodule, the pistillate inflorescences rarely exceeding 10 cm. in length, the flowers borne singly at each nodule, bracts minute, 0.5 mm., ovate, acute, puberulent, ocreolae large, 3–4 mm. long, membranaceous, bilobed, each lobe apiculate to acute, pedicels equaling or slightly exceeding the ocreolae, hypanthium 0.8 mm. long, narrowed to a stipe 0.5–1 mm. at the base, perianth lobes oblong-elliptic, 2 mm. long, fertile stamens longer than the lobes and exserted, fertile pistil 2 mm. long, styles 3, non-functional parts rudimentary; fruiting pedicels 3–4 mm. long, the fruit ovate, 1 cm. long, 8 mm. in diameter, the base rounded, short stalk evident, the apex obtusely acute, not coronate, the lobes imbricate and about ¼ the length of the fruit, smooth and not striate; achene chestnut brown, smooth, not trigonous.

Type: *Schomburgk s. n.* Rio Parimé, Brazil (Kew).

Collected in flower in June. Collected in fruit in June and August.

Panama, Colombia, Peru, Brazil. Altitude to 120 m.

CANAL ZONE: Barro Colorado Island, *Aviles 15*; *L. H. & E. Z. Bailey 219, 654*; *Bangham 447*; *Salvoza 904*; *Shattuck 1123*; *Standley 41099*; *Wetmore & Woodworth 859*. PANAMÁ: Juan Díaz region near Tapia river, *Maxon & Harvey 6700*.

6. COCCOLOBA UVIFERA (L.) L. Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera L. Sp. Pl. 365. 1753.
Guaiabara uvifera House, Amer. Midl. Nat. 8:64. 1922.

Tree of strand areas, 2–15 m. tall; branches stout, papillose to pilose; ocreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, papillose to pilose; leaves of normal shoots with stout petioles, 7–10 mm. long, puberulent to pilose, the blades orbicular to reniform, 10 × 10, 11 × 14, 13 × 18, 20 × 27 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe extending around the petiole, the primary veins 3–5 pairs usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, the secondary venation minutely reticulate or obscure; inflorescence stout, 15–30 cm. long, racemose, occasionally branched at the base, the rachis puberulent, staminate flowers in clusters of 1–7, the pistillate flowers solitary at each locus, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ocreolae membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long, fruit obpyriform, 1.2–2 cm. long, 8–10 mm. in diameter, narrowed at the base, rounded-truncate at the apex, the perianth rose-purple when mature; achene black.

Type: Linnaean Herbarium—(terminal leaf of young plant.) Jamaica (?)

Local name: "sea grape".

Collected in flower in January, February and October. Collected in fruit in March.

General in the West Indies, Mexico, Central and northern South America along beaches and strand locations.

BOCAS DEL TORO: Almirante, *G. Proctor Cooper 558*; Changuinola valley, *Cooper & Slater 82*; Chiriquí Lagoon, *von Wedel 2826*. PROVINCE UNKNOWN: Isthmus of Chagres, *Fendler 287*.

7. COCCOLOBA MANZANILLENSIS Beurling, Prim. Fl. Portobello in Kongl. Vetensk. Akad. Handl. Stockh. 142. 1854 (1856). (as *C. manzinellensis*); Lindau, Engl. Bot. Jahrb. 12:209. 1890.

Campderia nematostachya Griseb., Bonplandia 6:4. 1858.
Coccoloba nematostachya Lindau, Engl. Bot. Jahrb. 13:208. 1890.

Tree; branches striate, canescent, branchlets striate, silky pubescent; ocreae membranaceous to thinly coriaceous, divided to the middle, protracted in a long obtuse apex, to 4.5 cm. long, golden or tawny pubescent; petioles inserted at the base of the ocreae, 1–2 cm. long, canescent on the adaxial surface, short pilose elsewhere becoming glabrate; leaf blades oblong-elliptic, obovate or obovate-elliptic, apex short acuminate to rarely rounded, narrowed below the middle to a cordate or nearly rounded base, 11 × 6, 15 × 8, to 25 × 15 cm. long and wide, thin, coriaceous and flat when young, conspicuously undulate or bullate between the veins

when mature, margin reflexed, primary veins 14–17 on each side, generally glabrous but long pilose on the midrib; inflorescence terminal, the staminate 15–34 cm. long, the pistillate 20 cm. long, loosely flowered, all parts pilose, peduncle 1 cm. long, staminate flowers in clusters of 3 or 4, pistillate flowers borne singly at each nodule, bracts and ocreolae minute, to 0.5 cm. long, pilose, pedicels thin, about 1 mm. long, hypanthium campanulate, slightly stalked, 1 mm. long, the perianth lobes ovate, about 1 mm. long, fertile filaments 1.5 mm. long, exserted, fertile pistil 1.5 mm. long, styles 3, fruiting pedicels 1–1.5 mm. long, fruit ovoid, slightly stalked at the base, coronate at the apex, strongly striate when dry, 7 mm. long, 4 mm. thickest diameter; achene dark brown, strongly trigonous.

Local name: "Hueso" (ex Standley).

Collected in flower in January. Collected in fruit in June.

Endemic to Panama. Known altitude 10–20 m.

CANAL ZONE: Barro Colorado Island, *L. H. & E. Z. Bailey 42*; *Shattuck 425*; between Gatún and Lion Hill, *Pittier 2570*. COLÓN: Porto Bello, *Billberg 230, 234* (Holotype). DARIÉN: La Palma, *Pittier 6599*. PANAMÁ: Pacora, *Allen 3450*. PROVINCE UNKNOWN: *Andersson s. n.* (Type of *C. nematostachya* Griseb., GOET.)

The appearance of specimens assigned to this species vary considerably and depend on the period of collection. The leaves are apparently deciduous and young foliage appears with the flowers. Thus flowering specimens have smaller leaves of soft texture which turn black on drying. This is the condition of the type specimens of both species considered here. A few leaves of the Andersson collection, which is the type of *C. nematostachya*, are more mature and show the bullate characteristic also found in the fully mature leaves of the collection by Liberty Hyde and Ethel Zoe Bailey (number 42) which is the only collection known in fruit. The long ocreae and copious silky pubescence clearly mark this species.

The original spelling of *C. manzinellensis* by Beurling has been changed to *C. manzanillensis* by Lindau. While the island where Billberg collected the type specimen can not be located on modern maps, Beurling's intentions were obvious. Manzanillo, or "little apple" in Spanish, is commonly applied to the widespread and infamous strand plant *Hippomane manchineel.* Although Lindau failed to comment on his correction of an orthographic error or to cite the original spelling, it seems desirable to allow this correction to stand.

8. COCCOLOBA DARIENENSIS Howard, Jour. Arnold Arb. 40:195. 1959.

Tree, to 33 m. tall, d.b.h. 30 cm.; branches terete, glabrous; ocreae chartaceous, obliquely truncate, 1 cm. long, glandular (?) resinous, tightly appressed; petioles arising from the base of the ocreae, 7–11 mm. long, terete or canaliculate above, glabrous; blades narrowly oblong to lanceolate-oblong, acute to short acuminate at the apex, cuneate at the base, 10.5 $\times$ 3.5 to 14.5 $\times$ 5.0 cm. long and wide, thinly coriaceous, glabrous, primary veins 9 or 10 pairs, arcuate-ascending; inflorescence racemose, 8–14 cm. long, ocreolae membranaceous, bracts and ocreolae rarely puberulent and ciliate at the apex and margins; staminate flowers 3–4 per nodule, pedicels shorter than the ocreolae, perianth lobes oblong, 1–1.5 mm. long, glabrous, functional stamens 3 mm. long, sterile pistil rudimentary, 1 mm. long; pistillate

flower not known; fruiting pedicels 1–2 mm. long, exceeding the ocreolae, glabrous; fruit ovoid, 5–7 mm. long, 5 mm. in diameter, rounded at the base, obtusely trigonous at the apex, hypanthium scarcely evident, perianth lobes distinct to the base, imbricate, achene chestnut brown or black, dull or shiny.

Collected in flower in June. Collected in fruit in July and October.

DARIÉN: vicinity of Campamento Buena Vista, Río Chacunaque above confluence with Río Tuquesa, *Stern, Chambers, Dwyer & Ebinger 813, 813A*; trail between Cana and Boca de Cupe, vicinity of El Real, along road to Río Pirré, *Stern, Chambers, Dwyer & Ebinger 603*; Pinogana, *Allen 934* (Holotype GH).

The recent collections by Stern et al. have increased our knowledge of this species, previously known only from the type collection. These specimens substantiate the previously suggested differences from *Coccoloba acuminata.*

The common *Coccoloba venosa* of the West Indies, Central America (Mexico to Costa Rica) and South America (Venezuela and Colombia) is to be expected in Panama. It will be distinguished from the present species by the larger leaves, broadest above the middle and borne on shorter and thicker petioles, by the longer bracts of the inflorescence and the smaller and more pointed fruit with characteristically brilliantly colored fruiting perianth.

9. COCCOLOBA PADIFORMIS Meisner in DC Prodr. 14:166. 1856.

Tree to 13 m. tall; branches terete, glabrous; ocreae membranaceous, obliquely truncate, 1 cm. long; petiole arising from the base of the ocreae, canaliculate above, glabrous, 10–18 mm. long; leaf blades oblong to oblong-obovate, apex short acuminate, base narrowed or rounded, 9.5 × 3.5, 13 × 6 to 18 × 8 cm. long and wide on normal shoots, to 26 × 12 cm. on vigorous shoots, glabrous, coriaceous when mature, margins slightly recurved, lateral veins 9–11 on each side, arcuate, leaves deciduous, the young leaves bright red to clear yellow, not turning black on drying; inflorescence solitary or to three in a cluster, racemose, 3–6 cm. long, basal ocreae one to several, coriaceous, slightly apiculate, glabrous, rachis terete, crispose puberulent, bracts minute to 1 mm. long, glabrous or puberulent, ocreolae membranaceous, conical or flaring, 1 mm. long, staminate flowers 1 or 2 at each nodule, pistillate flowers solitary at each nodule, pedicels horizontally divergent, 2 mm. long, puberulent or glabrous, hypanthium short, 0.5–0.75 mm. long, perianth lobes ovate-oblong, 1 mm. long, fertile stamens with subulate filaments 2 mm. long, fertile pistil 2 mm. long; fruiting pedicels 3–5 mm. long, fruit globose, 8–9 mm. in diameter when dry, perianth lobes imbricate and distinct for ¼ to ⅓ the length of the fruit; achene pale green to tan, smooth and often shining, not coronate, hypanthium moderately veined when dry.

Type: *Moritz 377* along river Catuche near Caracas, Venezuela.

Costa Rica, Panama, Colombia, Venezuela.

CANAL ZONE: south of Fort Sherman, *Johnston 1737, 1814*; Quebrada Ancha, *Steyermark & Allen 17101*; vicinity of Río Cocoli, Road K-9, *Stern, Chambers, Dwyer & Ebinger 27, 28*; Gatún, *Pittier 2785.*

10. COCCOLOBA LEHMANNII Lindau, Engl. Bot. Jahrb., Beibl. 49:6–7. 1895.

Coccoloba lehmanni Lindau, Repert. Nov. Spec. Reg. Veg. 1:156. 1905.
Coccoloba changuinolana Standley, Pub. Field Mus. Nat. Hist. 8, 1:9. 1930.
Coccoloba williamsii Standley, Publ. Field Mus. Nat. Hist. 11, 5:148. 1936.
Coccoloba alleni Lundell, Contr. Univ. Mich. Herb. 6:8. 1941.

Small tree to 10 m. tall; branches sulcate, glabrate; ocreae 1–2 cm. long, membranaceous, mostly deciduous, minutely puberulent with or without resinous excretions, these often becoming numerous and appearing as lepidote scales; petioles arising from the base of the ocreae, 1–2 cm. long, canaliculate above puberulent and/or with resinous scales; leaf blades elliptic, elliptic-oblong, rarely oval-elliptic or obovate-elliptic, the apex short acuminate to acute or obtuse, the base rounded or shortly attenuate to the petiole, 9 × 4.5, 15 × 8, 17 × 10 to 20 × 12 cm. long and wide, thinly coriaceous, glabrous above except puberulent on the midrib, glabrous below or puberulent on the veins or occasionally with resinous excretion evident on the blade and veins, primary veins 10–17 on each side; inflorescence terminal or lateral, racemose, 10, 24, or to 35 cm. long, the peduncle 1–3 cm. long, the ocreae frequently flaring, membranaceous and conspicuous, to 5 cm. long, all parts puberulent or with resinous excretions, staminate flowers borne in clusters of 2–4, pistillate flowers borne singly at each nodule, flower clusters clearly distinct to nearly confluent, bracts triangular-ovate, the apex acute, 1–1.5 mm. long, the ocreolae membranaceous, split along one side and sheathing or equally divided into two flaring or erect lobes, usually membranaceous and conspicuous, 2–3 mm. long, flowering pedicels equaling or slightly shorter than the ocreolae, puberulent, hypanthium 1 mm. long, narrowly campanulate, perianth lobes round to oblong, about 2 mm. long and nearly as wide, functional stamens exserted on filaments, 2 mm. long, functional pistil 1.5 mm. long, styles 3; fruiting pedicels to 6 mm. long, exceeding the ocreolae, fruit ovoid, to 7 mm. long and 5 mm. in diameter, apex obtuse, base rounded, perianth lobes surrounding the achene, hypanthium not evident in fruit; achene light tan, strongly trigonous.

Type: Colombia, Dept. Antioquía, Cauca, *Lehmann 7560.* (lectotype Berlin).

Collected in flower in June and December. Collected in fruit in March and July.

Costa Rica, Panama, Colombia, Venezuela.

BOCAS DEL TORO: Changuinola valley, *Dunlap 499* (type of *C. changuinolana*); Daytonia farm, region of Almirante, *G. Proctor Cooper 421.* COCLÉ: El Valle, *Allen 2181* (type of *C. alleni*), *Allen & Alston 1857.* DARIÉN: Ensenada Guayabo, *Stern & Chambers 181.*

11. COCCOLOBA ACUMINATA HBK., Nov. Gen. 2:176. 1817.

Coccoloba strobulifera Meisner, Fl. Bras. V, 1:14, tab. 25. 1855.
Coccoloba acuminata var. *pubescens* Lindau, Engl. Bot. Jahrb. 13:193. 1890.
Coccoloba acuminata var. *glabra* Lindau, Engl. Bot. Jahrb. 13:194. 1890.

Shrub 1–2 m. or tree to 8 m. tall; stems smooth, puberulent to glabrate; ocreae membranaceous, 1 cm. long, truncate, puberulent to ferrugineous pilose or with glandular excretions; petioles arising from the base of the ocreae, 1–1.5 cm. long,

ferrugineous pilose, puberulent or glabrate; blades lanceolate, ovate-lanceolate or oblong lanceolate, acuminate at the apex, cuneate or almost rounded at the base, 11 × 4, 13 × 3.5, 17 × 6 to 24 × 7 cm. long and wide, subcoriaceous, dark green above and pale gray-green below when fresh, drying black and shiny above and dull opaque below, flat, pilose, puberulent to glabrate below, primary veins 13 to 20 on each side, crispose-pilose in the axils of the veins below, on the midrib or glabrate; inflorescence 15–29 cm. long, nodules distinct and separate, peduncle 2–4 cm. long, rachis pilose, puberulent or glabrate, angular, striate, expanding below each flower cluster, staminate flowers borne singly but subtended by a series of imbricate ocreolae or in clusters of 2–5 flowers each with a single ocreola, pistillate flowers generally borne singly, bracts ovate, acute to acuminate, puberulent, ocreolae membranaceous, puberulent, or pilose-ciliate on the margin, pedicels shorter than the ocreolae, to 1 mm. long, hypanthium campanulate to 1 mm. long, perianth lobes ovate, 1 mm. long, puberulent or glabrous, or with glandular excretions appearing as scales, fertile filaments to 1.5 mm. long, exserted, fertile pistil 1 mm. long, styles 2 or 3; fruit subglobose, strongly trigonous, attenuate at both ends, 6–8 mm. wide at the middle, perianth lobes surrounding ½ to ⅔ of the fruit, fruiting perianth fleshy, bright or dull red often white when fresh, black when dry; achene chestnut brown to pale tan, shiny, strongly trigonous.

Type: *Humboldt s. n.* near Mompox along Río Magdalena, Colombia.

Collected in flower in February and April. Collected in fruit in February, April, June, July, August and October.

Colombia, Ecuador, Peru, Venezuela, British Guiana, Brazil. Altitude 20–100 m. above sea level.

CANAL ZONE: Barro Colorado Island, *Aviles 74, 976, L. H. & E. Z. Bailey 616, Bangham 378, Starry 223, Wilson 22, 140, Woodworth & Vestal 397*; Juan Mina along Chagres River, *Bartlett & Lasser 16321*; Gamboa Beach, *Maggs II 39*; Frijoles, *Maxon 4707*; Gamboa, *Pittier 2608*; upper Chilibre River, *Seibert 1510*; Quebrada Bonita, *Steyermark & Allen 17194*. DARIÉN: vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern, Chambers, Dwyer & Ebinger 938*; Yape, *Allen 850*; Tucuti, Chepigana, *M. E. & R. A. Terry 1381*; without location, *MacBride 2676*; without province, Maune & Gorgone, *Wagner s. n.*; Marragantí, *Williams s. n.*; without location, *Weddell s. n.*

12. COCCOLOBA CARACASANA Meisner, DC Prodr. 14:157. 1856-57.

Coccoloba caracasana forma *glabra* Lindau, Engl. Bot. Jahrb. 13:211. 1890.

Tree 2.5–12 m. tall; branches sulcate, hispid pubescent to puberulent or glabrous; ocreae 1–2.5 cm. long, membranaceous, often spreading pubescent, puberulent, glabrous or covered with resinous excretions; petioles borne at the base of the ocreae, 1–2 cm. long, pilose to puberulent or glabrous; leaf blades oval, ovate or orbicular, rarely oblong or elliptic, the apex obtuse, rounded or emarginate, the base usually rounded and slightly cordate, rarely narrowed and acute, 6 × 6, 8.5 × 9, 12 × 14, 14 × 12 to 15 × 10.5 cm. long and wide, coriaceous, glabrous above, pilose or hispid below to puberulent or glabrous, the pubescence most commonly persistent in the axils of the veins or on or along the midrib, veins 10 or 11 on each side; leaves of adventitious shoots borne at the base of the ocreae

Fig. 108. *Coccoloba caracasana*

3.5 cm. long petioles to 4 cm. long with blades 37 × 25 cm. long and wide; inflorescence terminal, to 25 cm. long, the flowering nodes usually distinct, peduncle 2 cm. long, rachis pilose to puberulent, rarely glabrous, sulcate, bracts triangular, acute, 1 mm. long, pilose, ocreolae membranaceous and transparent, pilose to puberulent, spreading, staminate flowers in clusters of 3–4, pistillate flowers borne singly at each nodule, the rachis not swollen or directed below each flower cluster, hypanthium conical, pilose, 0.5 mm. long, the perianth lobes ovate, 1–1.5 mm. long and broad, the outer ones usually densely pilose, fertile stamens 1.5 mm. long, exserted, fertile pistil with exserted styles; fruit nearly globose, 5–6.5 mm. long, 5 mm. in diameter, the base rounded or narrowed to a short stalk when dry, the apex obtuse, the perianth lobes covering ⅔ of the achene or more, white when fresh, brown or black when dry; achene strongly trigonous, reddish-brown or black when fresh, dull dark brown when dry.

Type: Meisner did not select a type in describing this species. Only one (*Vargas 30**) of the many specimens he did cite is currently in the Prod. Herb. and this must be considered the lectotype.

Local names: "ubero", "papaturro blanco".

Collected in flower in February, March and April. Collected in fruit in April.

Mexico, Guatemala, El Salvador, Costa Rica, Nicaragua, Panama, Colombia, Venezuela.

CANAL ZONE: Ancón, *Pittier 2730*; Gorgas Memorial Lab., *White 106*; below Miraflores Dam, *Stern, Chambers, Dwyer & Ebinger 4*; Río Agua Salud near Frijoles, *Piper 5848*; Victoria Fill near Miraflores Locks, *Allen 1701*. CHIRIQUÍ: Progreso, *Cooper & Slater 270*. PANAMÁ: Sabanas Road, *Gillespie P-34, 34a*; Chepo, *Klug 25*. LOS SANTOS: La Jagua, *Bartlett & Lasser 16382*.

Collectors have noted this species to be infested with biting, stinging ants. None of the specimens seen has a hollow pith or sufficient pith for ant quarters, and I suspect that the ants may be in the ocreae sheaths. This is the only species in Panama reported to have a sweet and edible fruit. Most species of *Coccoloba* have astringent fruit.

6. TRIPLARIS Loefl.

TRIPLARIS Loefl. It. Hisp. 256. 1758.

Blochmannia Reichb. Consp. 163. 1828.
Velasquezia Bertol. Fl. Guat. 39. 1840.

Flowers dioecious, solitary or fasciculate in the ocreolae, short-pedicellate to subsessile, the pedicels, rhachises and dorsal surfaces of the ocreolae usually densely pubescent. Staminate flowers in fascicles of 1–5 subsessile pairs; tepals 6, subequal, linear to ovate, uniseriate, pubescent; stamens 9, exceeding the more or less campanulate tepals, the filaments discretely attached to the bases of the free portions of the tepals, not forming a distinct annular ring; anthers versatile, introrse, 4-locular; pistillodes absent. Pistillate flowers pedicellate and mostly solitary in the ochreolae; tepals in 2 strongly dissimilar series; outer 3 (sepals) connate at the bases forming a rhomboidal to campanulate tube, the distal portions

developing into oblanceolate wings; inner 3 (petals) much smaller, linear to ovate, free or partially adnate to the tube; staminodia absent or occasionally forming an annular disc from which apparently functional stamens arise; ovary trigonous; styles 3, with verrucose stigmatic tissue extending down their inner surfaces to about half their length. Achenes included, triquetrous or rarely terete, with a small beak formed of the persistent style bases, brown, lustrous or dull, occasionally verrucose or punctate. Trees with glabrous to densely tomentose or strigose hollow branches. Leaves alternate, entire, glabrous to densely tomentose or strigose, oblong to ovate, often slightly inequilateral, often with conspicuous longitudinal striae representing the plications of the leaf in the bud, the veins immersed above, but prominent below; ochreae deciduous. Inflorescences of predominantly terminal subspicate panicles or racemes.

Of this largely South American genus of some twenty species and fifty names, three species reach Panama, with only one reaching as far north as Mexico. Many species with bright red inflorescences are cultivated as ornamentals. Some have weedy tendencies and constitute important elements in secondary successions. Much to the collector's consternation, the hollow internodes are almost invariably inhabited by vicious ants. Recent workers have pointed out the urgent need for a monograph of the genus. No monographic work, except on a regional basis, has appeared since Meissner's monograph of the Polygonaceae (in DC. Prodr. 14:1–186. 1856.). The genus, like so many dioecious amentiferous groups, is badly complicated by specific intergradations.

A closely related largely South American genus *Ruprechtia,* which differs in having solid internodes and terete achenes, has been reported from Panama, but the report was based on vegetative material (Standley, in Contr. U. S. Nat. Herb. 27: 170. 1928.). I have seen no specimens of *Ruprechtia* from Panama.

a. Pistillate petals adnate to the calyx tube for 3 mm. or more, often auriculate or tubular near the peak of adnation, longer than the achene, mostly linear to spatulate; achene facies not sulcate; pedicels equaling or exceeding the ochreolae; hairs on the rhachis mostly less than 1 mm. long; staminate spikes more than 6 mm. broad, the tepals connate for at least half their length.

b. Leaves broadly ovate, about twice as long as broad, with about 15 pairs of lateral veins; pistillate petals adnate to the calyx tube for at least 6 mm., conspicuously exceeding the tube and distally dilated. 1. T. MELAENODENDRON

bb. Leaves oblong, 2–4 times as long as broad, with 17–30 pairs of lateral veins; pistillate petals adnate to the calyx tube for 2–5 mm., equaling or slightly exceeding the tube, not conspicuously dilated distally........ 2. T. CUMINGIANA

aa. Pistillate petals scarcely if at all adnate to the calyx tube, exauriculate, shorter than the achene, narrowly obovate; achene facies sulcate; pedicels mostly shorter than the ochreolae, hairs on the rhachises 2.5 mm. long; staminate spikes 5–6 mm. broad, the tepals connate less than half their length........ 3. T. AMERICANA

1. TRIPLARIS MELAENODENDRON (Bertol.) Standl. & Steyerm. in Field Mus. Bot. 23:5. 1943.

Velasquezia melaenodendron Bertol. Fl. Guat. 40. 1840.
Triplaris auriculata Meissn. in DC. Prodr. 14:174. 1856.
Triplaris Macombii Donn. Sm. in Bot. Gaz. 19:257. 1894.
Triplaris Macombii var. *rufescens* Donn. Sm. loc. cit. 20:293. 1895.

Fig. 109. Above: *Triplaris cumingiana,* habit and details; Lower right: *T. melaenodendron*; Lower left: *T. americana.*

Small trees up to 12 m. high, the upper branches geniculate, glabrous or appressed-pubescent, reddish to grayish brown. Leaves subsessile to petiolate, the petioles canaliculate and up to 2 cm. long; blades ovate, usually 1.5–2 times as long as broad, 15–30 cm. long, 8–18 cm. broad, apically acute to acuminate, basally rounded, densely appressed-pubescent or glabrous, with mostly less than 18 pairs of lateral veins. Staminate inflorescences of fascicles closely approximated along the rhachises forming compact spikes up to 1 cm. broad, the spikes simply or racemosely disposed; perianth in one series of 3 linear and 3 narrowly deltoid tepals, 4–4.5 mm. long, connate for over half their length; filaments about 7 mm. long, adnate to the tepals for 2–3 mm.; anthers 1–1.5 mm. long. Pistillate flowers with pedicels 3–9 mm. long, the sepals becoming 35–50 mm. long, the wings commonly only twice as long as the tubes; wings oblanceolate with rounded or subacute apices, with 1 conspicuous central vein from which several laterals arise, plicate just above the tubes; tubes more pubescent without than within; petals 15–30 (–40) mm. long, distally up to 3 mm. wide, usually adnate to the tubes for at least 6 mm., often auriculate or tubular near the peak of adnation; ovary trigonous; styles 3, 2–5 mm. long, their inner surfaces stigmatic. Achenes 9–12 mm. long, 5–8 mm. broad, dark yellowish brown; facies ovate, not sulcate.

This, the most common species north of Panama, is an inhabitant of low altitude thickets and forests. Ranging from Mexico to Colombia, it seems to grade into the more southern species *T. cumingiana*. *T. colombiana* Meissn., of northern Colombia, appears to differ only in having narrower leaves and asperulous-punctate achenes. *T. melaenodendron* has been reported from Panama and is to be expected there, but I have yet to see a specimen from Panama. Some common names applied to the tree in Central America are *hormigo, mulato, tabaco, tabacón, gallito, canilla de mula, palo mulato* and *tabaco de monte*. It is one of the most conspicuous elements of the flora of the Pacific Coast of Central America (fide Standl. & Steyerm. in Field Mus. Bot. 24^4:137. 1946).

2. TRIPLARIS CUMINGIANA Fischer & Meyer, in Mem. Acad. St. Petersb. 6^6:149. 1840.

? *Triplaris lindeniana* Wedd. in Ann. Sci. Nat. 3^{13}:266. 1849.

Small trees up to 15 m. high, the upper branches geniculate, usually glabrous, reddish to grayish brown. Leaves subsessile to petiolate, the petioles canaliculate and up to 2 cm. long; blades oblong, mostly 2.5–4 times as long as broad, 15–25 (–30) cm. long, 4–9 cm. wide, apically acute to acuminate, basally rounded to acute, glabrous except for the strigose midribs and occasionally the lateral veins below, with 18–30 pairs of lateral veins. Staminate inflorescences of fascicles closely approximated to the rhachises forming compact spikes up to 1 cm. broad, the spikes simply or racemosely disposed; perianth in one series of 3 linear and 3 narrowly deltoid tepals 3–4 mm. long, connate for about half their length; filaments 4–6 mm. long, adnate to the tepals for 1.5–2 mm.; anthers 1–1.5 mm. long. Pistillate flowers with pedicels 2.5–9 mm. long, the sepals becoming 30–50 mm. long, the free wings 2–3 times as long as the tubes; wings oblanceolate with

blunt to acute apices, 3-nerved, plicate just above the tube, the tubes more pubescent without than within; petals 12–18 mm. long, adnate to the tube for 2–5 mm., occasionally auriculate or tubular near the peak of adnation; ovary trigonous; styles 3, 2–5 mm. long, their inner surfaces stigmatic. Achenes 8–12 mm. long, 4–5 mm. broad, yellowish-brown; facies ovate, not sulcate, often strongly veined or verrucose.

CANAL ZONE: Between Mt. Hope and Santa Rita Trail, *Cowell 63*; Victoria Fill, near Miraflores Lock, *Allen 1700*; vicinity of former town Empire, Culebra Cut and vicinity, *Hunter & Allen 777*; Ft. Clayton, *Piper 6011*; Ft. Clayton, *Wheeler & Zetek in 1923*; Pa. Rr. Sta., *Sutton Hayes 971*; no spec. loc., *Christopherson 141*. DARIÉN: trail between Pinogana and Yaviza, *Allen 293*; R. Chucunaque, *Leopold 146*; along Interamerican Hwy. between Pinogana and Yaviza, 1 km. from Tuira, *Stern, Chambers et al. 126*; vicinity of Campamento Buena Vista, R. Chucunaque, above confluence with R. Tuquesa, *Stern, Chambers et al. 858*. PANAMÁ: Chiva-chiva Rd., 100 m., *Allen 4269*; Chepo, *Kluge 38*. SAN BLAS: Perme, *Cooper 644 & 647*. PROVINCE UNKNOWN: *Sutton Hayes 386*.

This, the commonly collected species in Panama, ranges from Costa Rica to Ecuador. In the West Indies and elsewhere it is cultivated as an ornamental. *Palo santo* and *guayabo hormiguero* are Panamanian names for the tree, the light-grained wood of which is occasionally used in construction.

Stern, Chambers et al. 858 is a particularly edifying collection. Although the tree was in fruit, the leaves were newly unfolding. The very young leaves are quite membranaceous and have 5–6 lines paralleling the midrib on either side. These lines represent folds incurred in the vernation in the strigose, fusiform terminal bud. Juvenile leaves are often unusually broad and may have fewer secondary veins, thus resulting perhaps in confusion with *T. melaenodendron.*

In Colombia *T. cumingiana* grades into closely related *T. surinamensis* Cham., which ranges from Colombia to Brazil, chiefly on the eastern half of the continent. *T. surinamensis* differs in having subglabrous rhachises, petals almost free of the calyx tube, and non-strigose foliar midribs, these often with a down tufted in the axils formed with the secondary veins. Intermediates between *T. cummingiana* and *T. surinamensis* are encountered and may possibly account for the obscure names *T. vahliana* Fischer & Meyer and *T. purdei* Meissner. In Ecuador *T. cumingiana* appears to grade into the larger-fruited *T. guayaquilensis* Wedd. (incl. *T. arnottiana* Meissner). *T. lindeniana* Wedd, with slightly narrower outer tepals, will probably prove, in a more concentrated study, to be conspecific with *T. cumingiana.*

3. TRIPLARIS AMERICANA L. Syst. 10:881. 1758-9.

Triplaris pyramidalis Jacq. Select. Stirp. Amer. Hist. 113. 1763.
Triplaris noli-tangere Wedd. in Ann. Sci. Nat. 3^{13}:264. 1850.
Triplaris felipensis Wedd. loc. cit. 3^{13}:263. 1850.
Triplaris pavonii Meissner, in DC. Prodr. 14:172. 1856.
Triplaris euryphylla Blake, in Contr. U. S. Nat. Herb. 20:239. 1919.
Triplaris laxa Blake, loc. cit. 20:240. 1919.

Small trees up to 20 m. high, the upper branches geniculate, glabrous to pubescent, mostly grayish-brown. Leaves mostly tapering to a petiole 1–4 cm. long and canaliculate; blades ovate, about twice as long as broad (in Panama),

15–30 cm. long, 7–15 cm. broad, apically abruptly acuminate, basally tapered, glabrous to hirsute on the veins below, with mostly 20–25 pairs of lateral veins. Staminate inflorescences of scattered fascicles forming lax spikes mostly less than 6 mm. broad, the spikes simply or racemosely disposed; perianth in 1 series of 6 narrowly ovate tepals 2 mm. long, 1 mm. broad, connate for about 0.5 mm.; filaments about 2 mm. long, adnate to the tepals for about 0.5 mm.; anthers about 0.5 mm. long. Pistillate flowers with pedicels 2–5 mm. long, sepals becoming 30–45 mm. long; wings mostly about 3 times as long as the tubes, oblanceolate with rounded apices, with 1 conspicuous vein from which several laterals arise, plicate just above the tubes; tubes as pilose within as without; petals 4–7 mm. long, 1–2 mm. broad, essentially free of the tubes, narrowly ovate to obovate; ovary trigonous; styles 3, 3–4 mm. long, their inner surfaces stigmatic. Achenes 7–8 mm. long, 3–5 mm. broad, yellowish brown, with a medial sulcation in which the petals fit.

DARIÉN: Marraganti and vicinity, 10–200 ft., *Williams 988*; vicinity Pinogana, 20 m., *Allen 4276*.

This variable species ranges from Panama to Brazil mostly at elevations below 900 meters and seems to be an important element in rain forests and in secondary successions. In Panama it is probably called *palo santo*; in Colombia it is called *vara santa*; in Peru, *tangarana* and *tangarana blanca*; in Brazil, *formigueira*.

Comparison of the achenes of the Panama material with those of the types of *T. felipensis, T. pavonii, T. williamsii* (in herb. N. Y. Bot. Gard.), and *T. euryphylla* and *T. laxa* (in U. S. Nat. Herb.) reveals that they possess in common the sulcate achenes as they are so clearly illustrated in the original description of *T. pyramidalis* Jacq. (Select. Stirp. Amer. Hist. pl. 173, fig. 5. 1763.). Dugand (in Mutisia 10:4. 1952) has correctly associated Colombian specimens with *T. pyramidalis,* and he indicates the close applicability of this name to the descriptions of *T. euryphylla* and *T. felipensis. T. williamsii* Rusby and *T. laxa* Blake are narrow-leaved variants perhaps worthy of specific designation. *Klug 2162* from Peru and *Krukoff 8330* from Brazil probably represent *T. bonplandiana* Wedd., which differs in having slightly sulcate, terete achenes and the petals occasionally lacking. *Ruprechtia martii* Meissner is very similar to and probably conspecific with *T. bonplandiana. T. brasiliana* Cham. (incl. *T. formicosa* Moore) represents a small-fruited departure from *T. americana. T. guanaiensis* Rusby* (incl. *T.*

* *T. guanaiensis* is involved in a species complex centering about *T. setosa* Rusby, a species with stiff pustulate hairs up to 1 cm. long. Britton (ex Rusby, in Bull. Torr. Bot. Club 27:130. 1900) described *T. hispida* from Bolivia. I believe this to be a hybrid between *T. guanaiensis* and *T. setosa.* In the same year Huber (in Bol. Mus. Goeldi 4:559. 1900) described *T. longifolia* from sterile material which had the distinctive hairs of *T. setosa* and might or might not be a hybrid. Then Rusby (in Mem. N. Y. Bot. Gard. 7:237. 1927) described *T. setosa* noting its affinity to *T. hispida.* Plants fitting *T. setosa* have long been passing as *T. poeppigiana* Wedd., but the type of *T. poeppigiana* has rhomboidal tubes with strongly plicate wings; furthermore it was described as having glabrous branches. The type of *T. setosa* contrasts sharply with its campanulate tubes with nonplicate wings and broad, round sinuses, and with pustulate hairs up to 1 cm. long. None of the Meissner types (in herb. N. Y. Bot. Gard.) and none of the Meissner descriptions (in DC. Prodr. 14:171. 1856) seems to resemble *T. setosa.* Standley (in Field Mus. Bot. 13^2:467. 1937) erroneously listed *T. setosa* as a synonym for *T. poeppigiana.* He also there described *T. punctata,* which seems to differ from *T. setosa* only in lacking the pustulate hairs.

boliviana Britton) differs slightly from *T. americana* in having lanceolate petals exceeding and masking the achene.

The name *T. americana* L. has long remained a mystery since the Linnaean description divulges no diagnostic secrets. A mysterious sheet, bearing only a fragment of a fruiting inflorescence, from the Bernhardi herbarium, which houses the type of *T. surinamensis,* is inscribed simply "Triplaris americana". This could very possibly be a fragment of the Linnaean type or a comparable specimen; the fruits are the same size as those in a microfiche of the Linnaean type. The leaves, as evidenced by the microfiche, are also identical with those of the specimens that I am treating as *T. americana.* A more firm substantiation of my claim, that *T. americana* and *T. pyramidalis* are conspecific, may be desired, but this would require a dissection of the Linnaean type. I sense no discomfort, however, in predicting* that such an operation would unclothe an achene with a groove in each of its three facies, and that in the groove or closely appressed to it will be a narrowly ovate or obovate petal, so characteristic of the extant Panamanian collections of what I here call *T. Americana* L.

* The prediction has already been fulfilled. In a letter dated Oct. 4, 1960, Prof. Dugand informs me that he has sent "nearly topotypical" *T. pyramidalis* to Sandwith for comparison with the type of *T. americana.* Dr. Sandwith confirmed Dugand's view that *T. americana* and *T. pyramidalis* are conspecific.

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